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Forest Insects and the Law of Natural Compensations[1]

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The subject of this paper was selected with enthusiasm. The law of natural compensations seemed most intriguing and the part played by forest insects in its enforcement appeared to afford unusual opportunity for discussion. Now that the time has arrived for its presentation there is a sense of trepidation, because the drawing of generalizations is always dangerous. However, without generalizations we should inevitably be confused by the mass of information concerning populations of insects, their parasites, predators, and host plants, and the responses of these organisms to their habitat. Therefore, it may be appropriate to present this somewhat old story from a different angle to illustrate the viewpoint of one forest entomologist, using some old and some hitherto unreported examples. Most of the examples that will be cited, whether old or new, have been observed first hand.

The operation of the law of natural compensations is far more easily seen in the forest than on farms or in orchards, where annual culture and harvest obscure the operation of natural forces. For this reason the forest entomologist is likely to be especially conscious of the actions, reactions, and interactions that go on in a community. He recognizes that some forest conditions are conducive to stability and relative safety from insect outbreaks and that other forests are unstable with a strong tendency toward periodic outbreaks of insects.

Statement of the law of natural compensations

Although it operates in all communities, it is in these unstable forests that the enforcement of the law of natural compensations is most conspicuous. The law may be stated very simply. If any species of plant or animal tends to dominate the locality in which it lives, either in number or influence, environmental forces will ultimately reduce it to a lower position. On the other hand, species few in number or weak in influence may be permitted to gain a more prominent place through the relaxation of limiting effects. Thus, in any community of living things compensating forces tend to keep each species in its appropriate proportion to others.

Insect outbreaks represent one of the natural forces which reduce aggressive tree species to a more appropriate position relative to other associated species. Parasites, predators, competition for suitable habitats, and other density-dependent influences prevent the pests from destroying all of their host trees. It is through these interactions that the law of natural compensations is enforced, thus contributing to greater stability and a more healthy situation. But before we take up specific examples of insects as compensators, let us first consider the forest and the conditions that contribute to stability or instability from a comprehensive viewpoint.

Stabilizing influences

Generally speaking, the degree of stability in a community is directly proportional to the number of species of which it is composed. In the moist tropical forests, characterized as they are by great complexity of species, insect outbreaks are very unusual. Only when cataclysms occur which simplify community

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composition do outbreaks develop. In temperate regions, however, only a few forest types are highly stable, and, as a result, resistant to insect outbreaks. Clearly complexity contributes to stability.

In Michigan, the mixed hardwood-hemlock forest is one of these. In that forest type hard maple and hemlock usually predominate but mixed with them in varying proportions are birches, elms, basswood, and ash, not to mention several subsidiary species such as ironwood, blue beech, and red oak. Some of these mixed, mature forests that we have studied show no evidence of serious insect injury throughout their life span of three hundred years or more. Nevertheless the number of insect species to be found there is far greater than in the less stable types. The great majority of the insect species are present in small numbers. Less than five per cent are conspicuously numerous at any time. A very sensitive balance produced by a combination of compensating influences must obviously exist to permit the major proportion of the species to persist year after year at a low level.

The details of the coactions in such stable forests have, thus far, never been studied as a whole. Only small segments have been investigated at any one time. Certainly continuing research studying any stable forest as a community would yield rich returns by contributing to a better general understanding of population dynamics.

We are far more likely, however, to devote our major research efforts toward the less stable types where outbreaks are most likely to occur, because it is there that problems of economic importance most often present themselves. Therefore, in this paper unstable conditions will receive most consideration because we know most about them.

Some of the less stable forests in which insect outbreaks are likely to occur have developed without interference by man. Natural forces operating within a community, such as competition between the various tree species, result in the gradual elimination of the poorer competitors. In the mixed hardwood-hemlock forest this results, at last, in stands of only hard maple on some sites, and hemlock on others.

Compensation by the hemlock looper

In this way a safe forest type is converted through the process of succession to an unsafe one. Then the operation of the law of natural compensations comes conspicuously into play. Pure or almost pure stands of hemlock are especially subject to insect damage which very often destroys them. The hemlock looper, by completely defoliating the trees in mid-summer, can kill hemlocks in a single season. This happened in Michigan and Wisconsin during the early twenties and completely changed the forest complex where complete defoliation occurred. The outbreak of the looper extended into forests where hemlock was mixed with hardwoods, but almost no trees were killed in forests that were composed of less than 50 per cent of mature hemlock. From this it is evident that compensations were not only operating against the hemlock, but also against the looper to prevent it from completely destroying its host.

Instability through cataclysms

We cannot study the forests for long without realizing that they are and always have been in a state of change. Some changes are the result of orderly succession; others are cataclysmic. An eternal battle goes on between the forces that encourage stability and those that lead to single species forests and instability. Usually the earliest successional stage is initiated by a cataclysm; forest fire, windstorm, logging operations, or a combination of these. We usually think

of man as being the greatest disturber, and in modern times perhaps he may be. Nevertheless, before he came to the North American continent, uncontrolled fires raged from time to time, and windstorms swept across the forest, leaving devastation in their wake. Although generalization in such matters is always dangerous, due to the many apparent exceptions encountered, we may safely say that physical cataclysms, especially fire, tend toward single species, unstable forests, whereas the stabilizing forces are usually biotic and compensating, encouraging greater diversification, either by species or by age classes.

Now let us consider a few illustrations that will show how the law of natural compensations operates in specific instances, and how forest insects play an important role in the enforcement of this law. The aspen forests of Michigan provide one good example of instability created by cataclysms.

Compensation in aspen stands

Aspen stands in Michigan, as in many other localities, are the direct result of logging and forest fires. Following pine logging in the latter part of the nineteenth and the early part of the present century, tremendous fires burned through the slashings, especially in the Lower Peninsula, destroying almost everything in their path and leaving the soil bare of vegetation. The covering of ash left from the burning debris provided an excellent seed-bed for many kinds of trees, especially aspens and paper birch.

Scattered pines and other heavy-seeded species, dropped their seed wherever a remnant of the older trees survived, and their progeny became established in many places. However, the fires were often so hot that no seed trees were left alive over extensive areas. These places were likely to be invaded by the light-seeded aspens or birches.

Perhaps even more frequently than through seeding, aspens reproduced themselves vegetatively, sending up root suckers for a distance of fifty to one-hundred feet around the dead stubs of parent trees killed by the fires. Until the virgin pine forests reached an age of about 125 years individual large aspen trees, contrary to common belief, were scattered among the pine. Following logging and fire these became the parents of sucker stands. The clones, thus established, spread slowly. A series of ground fires killed most of the pine reproduction and the above-ground parts of the aspen seedlings and suckers. The coniferous seedlings were lost, but the unkilled aspen roots sent up new suckers. With each successive fire, the suckers spread and more of the land was covered by them, and less and less by coniferous growth. By 1910, young aspens were the predominant forest cover on lands once occupied by the original pine-aspen-birch forests.

An intensive ecological study of aspens and their insect and vertebrate associates has recently been completed at the University of Michigan. In his doctoral dissertation, now in preparation, Robert Harrison, who participated in the study, presents much valuable information concerning aspen insects and their influence on the stands. The details cannot be released at present, but it can be said without infringing unduly upon his unpublished material, that insects are exerting an effective compensating influence upon the over-abundant aspen stands.

The sequence of this influence upon the aspen stands is most interesting. At about five years of age the suckers are attacked by a number of different insects, among them the gall-forming saperda, leafhoppers, aphids, the willow sawfly and at least two species of agrilus. The resultant mortality of part of the stand releases the residual trees, which then grow rapidly, until once again,

between 10 and 15 years they become too dense for rapid growth and are attacked by a variety of borers and sucking insects. For a second time the stands are thinned and the surviving trees released for another period of rapid growth. Still a third period of mortality follows between twenty and twenty-five years. The poplar borer is especially injurious at that time, opening in the trees infection courts for organisms causing cankers and decay. It is during this last period that the aspens become defective and the stage is set for complete deterioration between thirty-five and fifty years. The final process of deterioration is in progress at the present time, and the insects are playing their part as compensating influences, reducing the once over-abundant aspen stands to a more appropriate biological position. The aspen is being replaced by conifers in some places, a mixture of hardwood trees in others, or if trees do not invade the deteriorating stands, by herbacious or shrubby growth.

Balsam fir following aspen

In the Upper Peninsula of Michigan in contrast with the Lower Peninsula, although fires following pine logging were numerous, there were many localities where young pines, spruces, balsam fir, and other conifers survived in greater number than in the Lower Peninsula. They are now, after thirty to forty-five years, replacing the aspen. Balsam fir is the most abundant species and will, after another ten to twenty years, attain a dominant position. Again, a single tree species will have assumed control of the environment over extensive areas. Natural compensations may then be expected to come into play in a manner characteristic of such situations. Unless man takes a hand, and through logging utilizes the stands as they reach maturity, the agency most likely to be the compensating force is the spruce budworm.

This is not the first time that the sequence from aspen to balsam fir and spruce has occurred in northern Michigan. Evidence from the annual ring pattern of old spruces show reduced growth, similar to that caused by the spruce budworm, during a period immediately prior to 1880. If it had not been for the post-logging fires, the widespread development of a new generation of balsam fir by 1915 would have been expected. Instead, in Michigan this setting of the stage for another budworm outbreak was delayed when fires destroyed the fir reproduction that followed the 1880 outbreak.

In contrast the balsam fir stands in the north and northeastern parts of Minnesota were not destroyed by post-logging fires and over thousands of acres the tree developed to a dominant position prior to 1910. In 1912 a budworm outbreak began which, over a decade, destroyed the major part of the Minnesota fir forests. Today a similar situation is developing in the younger stands that survived.

From these facts we may logically conclude that repeated outbreaks of the budworm provide natural means for keeping balsam fir in its appropriate numerical position in relation to other species. Similarly, we know that equalizing forces in the form of parasites, predators, and nutritional conditions operate against the budworm to prevent it from completely destroying its host trees.

On the better sites, hardwood trees such as red maple, hard maple, and birches increase with each generation of balsam fir. This tendency leads toward greater stability. On sites where hardwoods are not invading, following the death of the balsam fir, the successional course is not clear. Except where fires have occurred, little, if any, proportional increase of spruce following a budworm outbreak has been demonstrated. Therefore, it seems reasonable to expect that successive periods of abundant mature balsam fir will be followed by budworm

outbreaks and temporary declines in susceptible balsam age classes. Possibly, after repeated oscillations, age-wise diversification might develop naturally within a locality, as a result of uneven mortality from place to place. Such inequalities could conceivably lead to local diversification of balsam fir age classes, until at last only a fraction of the trees in an area would be simultaneously in a mature condition.

Still another so-called fire type that has become very abundant illustrates the operation of compensatory forces. Jack pine now occupies much of the land in the Lake States that was once covered with red pine, and insect outbreaks of various kinds are frequent and, at times, severe.

According to early reports and the opinions of older foresters, jack pine, prior to 1920, suffered little insect injury. No less authority than Raphael Zon emphatically expressed the opinion that "Jack pine is the tree for the Lake States", because of its apparent resistance to fire and insects.

This opinion might have been correct under primitive conditions when jack pine forests occupied relatively restricted areas of land. But by 1920 the original pattern of spotty distribution had changed. Extensive and continuous stands of the tree had become established, following logging and forest fires, in places where red pine had grown before. Even while Zon was expressing himself concerning the desirability of the species, several serious insect pests were reaching outbreak proportions unobserved. The jack pine sawfly, then new to science, the black pine-leaf scale, the pine budworm, all joined forces to compensate for the dominance attained by the jack pine.

Some jack pine forests were killed by their combined attack, but before the tree could be reduced to its former state, other compensating factors reduced the numbers of its insect pests. Since 1920 repeated outbreaks of these and other insects have periodically appeared in jack pine stands. The pine tussock moth, the so-called anomola beetle, and the jack pine tortoise scale are among the more conspicuous of these, all relatively new pests. On the better sites natural invasion of other trees, supplemented by insect outbreaks, is reducing the area of jack pine forests, but on the poorer soils the struggle between the tree and its pests results in alternating dominance of first pines and then insects. This may be expected to continue until once again the pines have been reduced to normal numbers. Although several generations of trees may live and die before the end is attained, the trends seem clear and insects are exercising a major compensating influence.

Instability from the planting of pines

Let us return once more to the after effects of pine logging in the Lake States and see how man's awkward efforts to improve matters has actually made them worse. Again insects exercise a compensating influence.

The great post-logging fires that burned through almost every slashing, and the smaller but repeated ground fires that followed, destroyed all tree growth in many places, and created prairie-like openings, some of them miles in extent. During the same period optimistic settlers, looking upon every bit of land that had grown trees as being a potential farm, hopefully labored to clear other thousands of acres; only to be disappointed when they discovered that a crop or two of potatoes exhausted the light sandy soils.

The tragedy of blighted ambitions and land abandonment fell upon much of northern Michigan. Lands reverted to the State, were sold for taxes, only to be abandoned and revert again.

Lands that thus became State property, because no one wanted them, and similar lands acquired by the Federal Government, became the State and National

forests. Naturally the foresters who were entrusted with the management of these almost treeless forests set up as their first objective the reforestation of the vacant areas.

Forest nurseries were established and plantations were set out. Techniques for growing trees and planting them were improved from the grub-hoe slit to the tractor drawn plow, and the mechanical planting machine. By the middle thirties efficient procedures had been developed for a planting program on a production line basis. The Civilian Conservation Corps provided the manpower needed.

Naturally the species that could be grown most easily and planted most successfully, i.e., the pines, were produced and planted to the exclusion of most other trees. Earlier fear of the blister rust had almost eliminated white pine from the planting program. Thus red pine and jack pine were planted almost exclusively.

Foresters delighted in the press notices of the millions of young trees that were being set out on their vacant acres, and forest cover was being restored at an unbelievable rate. Block after block of open land was planted, resulting in thousands of contiguous acres of the same species. All this happened within the span of a few years, so that the pure stands of pine were predominantly in the same age class. As long as funds for the Civilian Conservation Corps were available, and in spite of warning from forest entomologists of what the results might be, the planting program continued.

Perhaps it was fortunate that some of the plantations were failures, the trees succumbing to drought and white grubs. Some breaks were thus made in the almost continuous plantations. But a large proportion were successful and have become established. Many have grown beautifully and are today a delight to any forester's eye. Others have not grown so well, and some have been dismal failures. Nevertheless, the planting program must be looked upon as a great success, since it re-clothed with trees millions of devastated acres.

Compensatory insects in pine plantations

But along with this success we are now faced by the penalties that must be paid for excessive planting of red and jack pines. Red pine now dominates vast areas, where once it grew in groups interspersed with other trees. Under these conditions created by man the operation of compensating forces is inevitable, and insects have been and are among the compensating agents.

As in the case of jack pine, early foresters commented upon the outstanding immunity of red pine to insects and diseases, and a feeling that this was true was common among younger foresters. It was not surprising to the forest entomologist, however, when pest after pest appeared in the red pine plantations. Similarly old enemies became more conspicuous than they had ever been before. Frequently the same insects were to be observed in large numbers both on red and jack pine. Therefore, both species may appropriately be considered together.

Insects that do not kill the trees but cause injury in terms of deformity and growth reduction became far more numerous in plantations than they had been in natural stands of reproduction. Among these may be mentioned the pitch blister moth and several species of stem miners. The white pine weevil shifted its attention increasingly from its more usual hosts to jack pine and still more recently to red pine. Some preliminary tests indicate that it still prefers white pine if given a free choice, but nevertheless heavy populations have built up in many red pine plantations. Individual leading shoots of red pine can provide for the development of fifty or more adult weevils, far above the usual rate of increase in white pine.

Since they do not kill the trees attacked, the group of plantation insects that we have been considering exercise their compensating effects only indirectly. Sometimes the chief effect is to stunt growth of the trees, particularly in height, thus enabling other tree associates, that usually grow more slowly than the pines, to occupy the site and ultimately kill the pines by suppression as they close in above them. Or, in other cases the injured trees may be attacked and killed by bark beetles. Actually, the indirect effects of these insects that injure but do not kill the trees is greater than is suggested at first glance.

Red-headed pine sawfly

More apparent, however, are the activities of insects that kill the trees outright, thus directly reducing the area occupied by man-made red and jack pine plantations. Several sawflies, but especially the red-headed pine sawfly, fall into this category. Its potentialities are illustrated in the Pigeon River State Forests in the Lower Peninsula of Michigan, where in one year it killed sixteen continguous plantations of jack pine.

Since the advent of DDT the cost of spraying has been materially reduced and spraying, at least in part, has thus far prevented any great upswing in the sawfly numbers. Later in this paper some of the biological implications of such spraying operations will be touched upon.

The Saratoga spittle bug

One insect that was almost unknown prior to 1940 has since then come into great prominence as a killer of planted pines. Until it was recognized as an insect of economic importance, the Saratoga spittle bug had been rare in insect collections and very little was known of its habits.

When the killing of branches by this bug was first observed it was erroneously attributed by some foresters to the white pine weevil. On the Manistee National Forest a control project consisting of clipping and burning the injured tips had been started. Inspection by forest entomologists disclosed, however, that a sucking insect was causing the damage, and the following year Secrest determined the identify of the culprit.

Only during the adult stage does the insect feed upon the pines. After a preoviposition feeding period the eggs are laid on the trees. When they hatch the young drop to the ground where the nymphs feed on plants of the ground cover; especially sweet fern, but also on briers and some herbaceous plants. Even during that stage they are inconspicuous, feeding on the host plants immediately above the mineral soil and beneath the litter of needles, grass, and twigs, that covers the ground. There, during June and early July, by parting the litter to expose the base of the stem, they may be seen feeding beneath the mass of spittle-like exudate.

When an adult spittle bug feeds on the pine tips a small necrotic spot develops in the cambium region about each puncture. When these spots are numerous they interfere with the movement of fluids in the stems. After a number of successive years of injury flagged twigs become numerous and ultimately the tree will be killed.

If it had been left uncontrolled, the Saratoga spittle bug would by this time have destroyed many of the jack and red pine plantations growing on sweet fern lands. Theoretically this should have created safer conditions by separating the insects from their favorite nymphal food, the sweet fern. It seems unlikely that the currently high populations could have been maintained without a combination of pines with sweet fern in close association.

Because sweet fern lands are of marginal quality the question might well be asked, looking at the situation from a long time viewpoint, why were pine

planted there in the first place, and secondly why was it justifiable to protect them by spraying, thus maintaining an unstable situation that the spittle bug promised to correct? From the immediate viewpoint, however, sprays were applied to protect the investment in the plantations that were being injured. The idea was that the insects could not again build up to outbreak numbers before the trees had closed together into solid stands, thus killing the ground cover and eliminating the nymphal food. The correct answer in cases of this sort cannot be judged with certainty in advance and only time will tell whether the short-term or the long-term viewpoint is to be preferred. In the meantime there will be ample opportunity for argument.

The Nantucket pine moth

An especially interesting example of how compensating forces work in plantations of pine may be seen in the Nebraska National Forest. There the planted pines have been severely injured by the Nantucket pine moth. The insect during the early twenties had become so numerous in the Nebraska plantations that the buds on practically every branch tip were mined and killed. Thus the trees were unable to grow in height. Instead of maintaining their characteristic conical shape they became globose, producing foliage from adventitious buds developed from each of the more distal leaf fascicles.

As in many other similar cases the compensating agent operating against the pines had itself gotten out of hand. Parasites were introduced from the Black Hills and from Virginia. One became established. This was *Campoplex frustranae* an especially desirable parasite in Virginia, according to Cushman. The parasite increased and spread at an astounding rate. Within three years it had reduced the tipmoth numbers to a minimum, the trees again were able to increase in height and once more they assumed the dominant place in the environment. But this was not for long, as we shall see.

While the pine moth was being studied prior to the establishment of campoplex a tipmoth of a second species, *Rhyacionia neomexicana*, appeared occasionally in our tipmoth rearings. Following the reduction in number of the original moth the southwestern species increased and severely damaged the pines, thus filling the niche left vacant. Nature, in this way continued to enforce her law of compensations by utilizing another agent in the place of the one that had become ineffective.

At that point in the chain of events our entomological study of the Nebraska plantations was brought to a close. During the twenty-five years between 1930 and 1955 a period of economic depression and two wars have occupied our attention and only reports from casual observations continue the story of pines and tipmoths. From these reports it appears that the Nantucket pine moth later increased in number and became the predominant species once more, causing severe injury to the pines. More recently DDT has been applied, and, according to some informal reports, the pines at first received considerable protection thereby. Later treatments, however, were less effective. Today the Nantucket pine moth predominates, *R. neomexicana* appears to be more numerous than it was originally, and Campoplex, though reported to be still present, has become ineffective as a control agency.

The story of the events that we have briefly outlined is most unsatisfactory. It bears some similarity to certain modern novels that bring us to the critical point in the lives of the heroes and heroines, only to leave us dangling between tragedy and comedy. What interplay of forces produced the results that have been reported so inadequately during the twenty-five years between 1930 and 1955? Why did campoplex cease to hold down the Nantucket pine moth popu-

lation? What has been the overall effect of the insecticide application? These questions can only be answered through careful studies conducted over many years. Only in this way can we hope to understand the interplay of environmental forces.

Chemical treatment and stability

For man's long-time best interest a reasonable amount of stability of the environment upon which his life depends is of paramount importance. Alternating periods of scarcity and abundance are not to be desired and are the fruits of instability. Therefore, we should be interested in encouraging stability instead of upsetting it as we sometimes seem inclined to do. At the same time, we must recognize that intensive culture of any crop precludes the possibility of attaining stability entirely by natural means. Compensating factors eliminated by culture must be replaced by others if stability is to be attained under the artificial conditions required for crops.

Therefore, where we create unnatural conditions, either on farm or in forest, direct and immediate action must often be taken to protect economic values. Chemical control illustrates the application of such prompt corrective practice. It should not be forgotten, however, that there are numerous instances where the necessity for chemical treatments might have been avoided through applying other procedures in advance. This is especially true in the forest, where careful planning of planting programs might have avoided some insect problems that have resulted from our disregard of the law of natural compensations. Through ignorance and poor planning the forester finds himself on the horns of a dilemma. He must either lose some of the plantations that have been established or he must take direct action to prevent insects from enforcing the laws of nature. Usually, he will chose the second alternative if the insect is one that can be controlled with an insecticide.

Whether or not such a decision is wise will depend upon circumstances. The deciding factors will usually be financial. Obviously, if by spraying we save needed products that are greater in value than the cost, the treatment is justified. But the problem may not be so simple. How much will be lost or saved cannot always be forecast accurately. Neither can the need for repeated treatments be accurately determined. To spray or not to spray is a decision requiring good judgment and usually more information about conditions than is available. It is not the purpose of this paper to discuss the pros and cons of chemical control of forest pests, but in considering the law of natural compensations the influence of such treatments upon the operation of this law deserves attention.

If insect oubreaks are nature's way of compensating for the over-abundance of any age class of a tree species, one thing seems certain. Elimination of the compensating insect population will leave the environment still unstable. Under such circumstances we should expect that the removal of one pest would be followed by the up-surge of another compensating species.

There is some evidence that this has happened following the application of DDT to the forest; not invariably but frequently enough to deserve consideration. It must be recognized, however, that the replacement of a pest population reduced through application of an insecticide is not exactly comparable with the substitution of the one tipmoth for the other, that has already been mentioned. In that instance the second species was ecologically the equivalent of the first and merely filled the space left vacant in the environment. When insecticidal treatments are followed by the upswing of certain insect populations, the insects

concerned need not necessarily be ecological equivalents of the one controlled by the insecticide.

Insecticidal effects cannot, in their very nature, be restricted to the pest against which they are applied. As a result, complex changes may follow their application. The evaluation of these effects is difficult and calls for far more intensive study than they have ever received. Therefore, at present, most of our assumptions regarding the environmental changes that follow insecticidal treatments are unproved. The result has been the formulation of conflicting hypotheses, that have not been tested. At times entomologists have enthusiastically defended their respective hypotheses without too much evidence on either side.

About as far as we can safely go is, on the one side to admit that insecticides do influence the environment by eliminating some of the compensating influences, and on the other side that such disturbance is likely to be transient following a single moderate treatment or a series of treatments each separated by a number of years. Therefore, we should not condemn the application of insecticides needed to meet a specific emergency, but neither should we regard insecticides as being the final word in forest insect control.

The most conspicuous population changes that have followed a single application of a poison such as DDT to forest populations have been the increase of some sucking insects such as scales, aphids, and perhaps leafhoppers. But other less conspicuous increases also seem to be taking place. A number of tip miners, the pitch-blister moth, and some pitch midges have increased appreciably in abundance since spraying for the control of plantation insects has become general. We cannot be sure however, whether the changes represent the compensatory filling of a void left by reduction of the pest population, or whether the changes are due to a reduction in the number of parasites and predators killed by the spray. But whatever the reason, the reaction must be compensatory in character, the insects responding either to an abundance of the plants they live upon or a scarcity of the organisms that live on them.

Conclusions

From our observation of forest environments, it is clear that compensating influences operate inevitably to prevent either plants or animal species from remaining too numerous or powerful in proportion to their associates. The important question now is, what does this mean to us as entomologists, foresters, and land managers generally?

The answer seems obvious. Instead of defying the law of natural compensations, as we often have done, we should plan our forest operations and our silvicultural practices to conform with the law. Insofar as we can, we should encourage diversity in forest composition. This may be accomplished either by encouraging multiple species stands or by limiting the size of areas occupied by the same age class of the same species. Thus diversification may be attained either species-wise or age-wise.

If for practical reasons we find that diversification to a desirable degree cannot be attained we must be prepared to substitute regulating forces of our own for those that we have eliminated. Intelligent chemical treatment might conceivably be one of these.

When we resort to the application of chemicals we should recognize that we are in no way adding to the permanent stability of the forest community, but are merely meeting an emergency, the justification for which can only be measured in financial terms. In the long run, we shall be faced with two alternatives: either to use increasingly intensive practices in growing trees, or to

adapt our practices to harmonize with the requirements of natural laws. The first will be expensive, the latter relatively inexpensive. The desirability of following nature seems evident, but to do so with greatest effectiveness will require more knowledge and understanding of the interplay of forces within the forest community than we now possess. In order to gain this knowledge, long-time research on a community level is essential.

Instead of concentrating attention upon a single insect that happens to be currently injurious, it will be necessary to view the forest community as a whole if we are to appreciate the significance of the actions, reactions, and coactions that make it what it is. Too much specialization of effort in such research may not be conducive to best results, but on the other hand superficiality cannot be condoned. Therefore, we should work toward a co-operative approach using specialists whose efforts are co-ordinated by one who possesses a broad grasp of the entire problem.

Until the results of this idealistic approach are available we can employ forest practices that seem most likely to conform with requirements for environmental stability. These practices will be accomplished mostly through the use of axe and saw. While we move toward safer practices we should never forget that the law of natural compensations will inevitably operate, sometimes to our economic woe, when one age class of one tree species tends to dominate a forest.

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A Simple Air-Conditioning Unit for Insect Cages[1]

By W. Haliburton[2] and W. G. Friend[3]

Attempts to maintain large cultures of the onion maggot, *Hylemya antiqua* (Mg.), have led to the development of special glass cages (Perron *et al.*, 1953). Under our laboratory conditions the lights used to obtain the degree of illumination necessary for acceptable oviposition rates raised the temperature and lowered the humidity excessively within the cage. Reasonable control of these factors was obtained by atomizing cold water into a current of air blown through the cage.

The apparatus consists of a sheet-copper box 16 inches long, 20 inches wide by 6 inches deep where it is joined to the cage, and 4 inches wide by 10 inches deep at the distal end (Fig. 1 a, b). Two glass low-delivery atomizers (Fig. 1 c), connected to a controlled air-pressure line, are mounted in the distal end of the box with their aspirating tubes immersed in circulating cold water, and are oriented so that their spray pattern covers the wide opening leading into the cage (Fig. 1 b). A glass marquisette* screen prevents the flies from entering the unit. An 8-inch opening in the top of the box is fitted with a hinged cover (Fig. 1 a) that allows access to the atomizers and also serves as an adjustable air vent. The interior of the box is coated with asphalt paint to minimize the level of copper in solution in the apparatus.

In operation, most of the larger spray particles impinge on the walls of the box, and only a fine mist is blown in along the roof of the cage. This mist falls

[1]Contribution No. 260, Forest Biology Division, and No. 3372, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.
[2]Chemical Control Section, Forest Biology Division, Ottawa, Ontario.
[3]Vegetable Insect Section, Entomology Laboratory, Ottawa, Ontario.
*30 mesh, mfg. by Hess, Goldsmith & Co., New York.

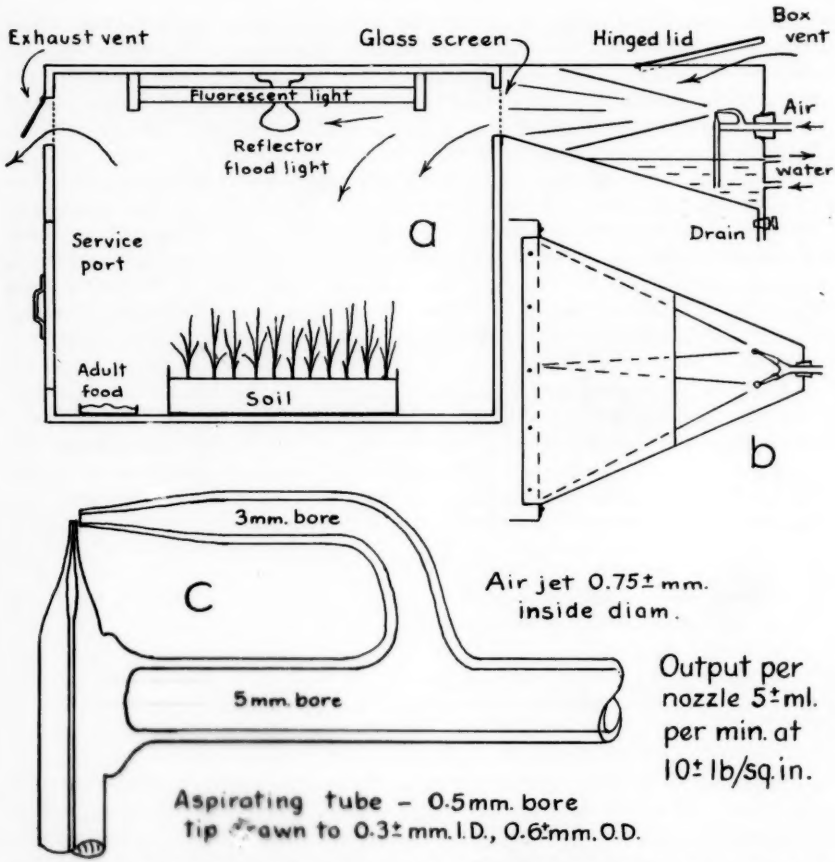

Fig. 1. *a* Profile diagram of cage and attached air-conditioning unit; *b* plan view of unit, hinged cover removed, showing distribution of spray pattern; *c* detail of atomizer nozzle.

slowly and evaporates rapidly. Adjustments of temperature and humidity are effected by manipulating the air pressure, the water temperature, and the cage and box vents (Fig. 1 a) that control the amount of air flowing through the cage. If necessary, additional air flow can be obtained by using an auxiliary air jet in the box or an exhaust fan at the cage vent.

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Perron, J. P., J. Lafrance and N. Hudon (1953). Notes on the behaviour of the adult of the onion maggot, *Hylemya antiqua* (Meig.), in captivity. 32nd and 33rd. Ann. Repts. Que. Soc. Prot. Plants, 1950-51, pp. 144-148.

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The Amino Acids Required for Egg Production in *Aedes aegypti*[1]

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Since the monumental work of Rose (1938) on the essential amino acids for growth in the rat, similar studies have been made on other vertebrates. It has been shown that most of these animals have the same pattern of amino acid requirements for growth of the immature form and for maintenance of nitrogen equilibrium in the adult. The amino acids usually required are arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophane, and valine. These studies have been adequately reviewed in recent texts (Bourne and Kidder 1953, Albanese 1950).

Amino acids essential for growth have also been determined in a number of insects. Chief among these studies are work on *Drosophila melanogaster* (Van't Hoog 1935, Lafon 1939, Hinton *et al* 1951), *Aedes aegypti* larvae (Golberg and De Meillon 1948), *Attagenus* sp. (Moore 1946), *Tribolium confusum* (Lemonde and Bernard 1951), *Blattella germanica* (House 1949), and *Pseudosarcophaga affinis* (House 1954).

The studies which have been cited have all concerned growth or maintenance of nitrogen balance of entire organisms. In many species, it has been impossible to study *in vivo* the effects of diet on specific tissues or specific processes since elimination of essential amino acids would result in abnormal protein metabolism of the organism or death.

The adult mosquito, however, offers an excellent subject for the study of the protein requirements for a specific process or complex of processes, that of egg production, and for growth of a specific tissue, the ovary, in that this insect can maintain apparently normal metabolism in the absence of dietary nitrogenous material but requires protein for the development of eggs. Thus, the needs for maintenance and for reproduction can be separated and studied independently. Experiments on the amino acid requirements for reproduction in female *Aedes aegypti* are described in this paper.

Previous studies on amino acid requirements for reproductive phenomena have concerned chiefly the observation of testicular atrophy or impairment in various vertebrates fed amino acid deficient diets. Greenberg (1951) showed that the amino acid isoleucine was probably required by *Aedes aegypti* for egg production. Preliminary experiments leading to the present study are described in the following papers: Lea *et al* (1955) and Dimond *et al* (1955).

Methods

The adult mosquitoes used to evaluate amino acid diets were reared and maintained under standard conditions of temperature and humidity. After emergence, the adults were held for 4 days on a 10 percent glucose diet, then inactivated with low temperature and counted into test cages in groups of 400 females.

Diets were prepared as solutions in water and contained only chemically defined ingredients. Other than the amino acids, all diets contained 5 grams per 100 ml. each of fructose and glucose, 0.15 grams per 100 ml. of a salt mixture, and sufficient sodium hydroxide to neutralize the solutions.

The mosquitoes were fed from cotton pads which were saturated with the experimental media. These pads were replaced in the cages daily. Each cage

[1]This investigation was supported by a research grant G1888 (C6) from the National Institutes of Health, Public Health Service.

also contained an oviposition dish from which the eggs were removed daily and counted. Counts were made over a period of 14 days after the initial feeding. The total egg production after 14 days from the cages of 400 females served as the basis for comparison of the experimental diets.

The steps followed in studying the amino acid requirements of the mosquito involved (1) determining the essential acids by eliminating each acid singly from a mixture of 13 and observing the effects on egg production, (2) finding the optimum mixture of the essential acids by varying the concentrations of single acids within a standard mixture and combining the levels which resulted in the highest production of eggs, and (3) studying some relationships between the essential acids and the non-essential acids, related compounds, and the sterioisomers of essential acids, by making substitutions in or additions to the optimum medium.

Results

Egg production from a basic mixture of 13 amino acids compared with production when single amino acids were omitted is summarized in Table I. Eight of the acids (arginine, isoleucine, leucine, lysine, phenylalanine, threonine, tryptophane, valine), when eliminated, resulted in the production of no eggs, and were therefore designated as absolutely essential for egg production. Four others (histidine, glutamic acid, cystine, methionine), when omitted, resulted in a significant decrease in egg production, although some eggs were produced. This latter group appears similar in status to arginine in the nutrition of the young rat where some of the acid is synthesized but not in sufficient quantities for optimum growth. With histidine and methionine in the mosquito, however, this is not the case apparently, since those few eggs which are produced, are laid during the first few days of the experiment, none appearing thereafter. It might be concluded that the deficient acid is carried over from the pupa in sufficient amount for the production of a few eggs. When these stores are depleted, the acid in question becomes unequivocally essential since in its absence, no further egg production will occur. On this basis, there seems to be no grounds for distinction between the essentiality of the eight absolutely required acids and histidine and methionine. In tests which will be described later, it was found that cystine was essential for optimum egg production, but that glutamic acid could be considered non-essential. Thus, 11 amino acids were found to be essential for a high level of egg production in *Aedes aegypti*, the eight acids required for the production of any eggs at all, plus histidine, methionine, and cystine.

The basic mixture for these experiments contained only 13 amino acids as it had been found in a preliminary test that this diet resulted in egg production equal to that from a mixture of 18 acids. Thus, five nonessential acids were found, alpha alanine, aspartic acid, proline, serine, and tyrosine. That glycine can be added to the group of non-essentials is indicated in Table I.

Results of the second phase of the experimentation, the establishment of the optimum mixture of essential amino acids for egg production in this mosquito, are given in Table II. With each medium listed, dose-effect data were obtained for each acid individually. The optimum concentrations of each acid for egg production were combined to form the next successive medium. No improvement could be made in Medium D through further change in concentrations. Egg production in the final medium was more than double that from the original basic diet while the total weight of amino acids was lowered about 25 percent. This serves to illustrate the importance of proper balance between the components of an amino acid mixture.

TABLE I

The effect of diets deficient in single amino acids on egg production from *Aedes aegypti*. Figures represent total egg production from 400 females after 14 days, and are averages of at least two replicates.

Diet	No. Eggs
Control Diet (Medium A, Table II)	6,961
" " minus Arginine	0
" " " Cystine	3,919*
" " " Glutamic acid	1,595*
" " " Glycine	6,649**
" " " Histidine	140*
" " " Isoleucine	0
" " " Leucine	0
" " " Lysine	0
" " " Methionine	872*
" " " Phenylalanine	0
" " " Threonine	0
" " " Tryptophane	0
" " " Valine	0

*Significantly different from the control at the 0.01 percent level according to a test of mean difference using the t-distribution.
**Not significantly different.

Following the establishment of the optimum mixture, the ability of the mosquitoes to utilize the unnaturally occurring isomers of the D configuration of some of the essential acids was studied. The D isomer of histidine appeared to be as effective as the L isomer in promoting egg production. The D isomers of methionine, phenylalanine, and tryptophane also could be utilized towards egg production, however, these were considerably less effective than the corresponding L forms. With isoleucine, leucine, threonine, and valine, substitution of the D forms resulted in the production of no eggs, and they therefore appeared non-usable.

Results of tests in which some relationships between essential acids and some non-essential acids and related compounds were demonstrated are summarized in Table III. From these miscellaneous tests it was found that citrulline could

TABLE II

Steps in establishing an optimum mixture of essential amino acids for egg production in *Aedes aegypti*. Values are in grams, 100 ml. of diet.

	Medium A	Medium B	Medium C	Medium D
L Arginine monoHC1	0.50	0.38	0.38	0.38
L Cystine	0.20	0.20	0.15	0.15
L Glutamic acid	1.00	1.00	1.00	1.00
L Histidine monoHC1	0.70	0.09	0.12	0.15
DL Isoleucine	1.00	0.50	0.50	0.50
L Leucine	1.00	0.75	0.75	0.75
L Lysine monoHC1	0.90	1.35	0.75	0.75
DL Methionine	0.20	0.15	0.15	0.15
DL Phenylalanine	0.70	1.20	1.20	1.20
DL Threonine	0.80	0.40	0.30	0.30
L Thryptophane	0.40	0.30	0.30	0.30
DL Valine	1.00	2.00	1.50	1.00
Glycine anhydride	0.50	—	—	—
Total grams	8.90	8.24	7.70	6.64
Egg production*	7,000	8,500	13,000	16,000

*Figures represent total egg production from 400 females after 14 days. They are averages of at least two replicates.

TABLE III

Results of tests in which the ability of *Aedes aegypti* to utilize some non-essential amino acids and related materials in place of essential acids was tested. Figure are total eggs from 400 females after 14 days.

Diet	No. Eggs
Control Diet (Medium A, Table II)	7,000
" " minus Arginine	0
" " " " plus Citrulline	3,380
" " " " " Ornithine	0
Control Diet (Medium D, Table II)	16,144
" " minus Glutamic acid	9,253*
" " " " " plus Aspartic acid	17,454**
" " " " " " Ammonium acetate	17,490**
" " " " " " Alpha ketoglutaric acid	10,975*
Control Diet (Medium D, Table II)	16,144
" " minus Cystine (0.15 gms Methionine)	11,852*
" " " " (0.30 " ")	13,707*
" " " " (0.45 " ")	12,097*
" " " " (0.50 " ")	12,090*
" " " " (1.10 " ")	12,400*

*Significantly different from the control at the 0.01 percent level according to a test of mean difference using the t-distribution.
**Not significantly different.

replace arginine in the diet in part, but that ornithine had no such effect. The interrelationships of these three amino acids, which participate in reactions known as the ornithine cycle of urea formation in vertebrates, have been studied in a number of organisms with similar results. (Hinton *et al* 1951, Rose 1938).

The stimulatory action of glutamic acid on egg production could be matched by the addition of aspartic acid or ammonium acetate to a mixture lacking glutamic acid. Apparently the effect of glutamic acid was principally due to its contribution of ammonia for the synthesis of non-essential acids. Further evidence towards this view existed in the fact that alpha ketoglutaric acid, the deamination product of glutamic acid, had no stimulatory effect. On this basis, glutamic acid was eliminated from the list of essential acids for egg production in *Aedes aegypti*. The fact remained, however, that a source of amino groups was stimulatory whether presented as glutamic acid or in some other form.

The status of cystine as an essential was also in doubt as workers studying the rat and other mammals have shown that it can be entirely replaced in the diet by an excess of methionine. This could not be demonstrated in the mosquito as is shown in Table III; the loss in egg production occasioned by the absence of cystine in the diets remained the same regardless of the level of methionine present. This is not surprising as a cystine requirement for growth has been demonstrated in several insects. (Golberg and De Meillon 1948, Hinton *et al* 1951).

Some further testing has concerned attempts to increase the level of egg production obtained with the essential amino acids by adding the non-essential acids. Investigations on several organisms, which include some insects, have shown that growth can be increased considerably by adding several non-essentials to a basic mixture of essential acids. The same was found to be true in promoting egg production in the mosquito if additions were made to a quantitatively sub-optimal mixture of essential acids, however, no improvement could be made in the optimum medium through the additions of non-essentials in groups or singly.

The effectiveness of the amino acid mixtures in promoting egg production as compared with blood is a point that bears discussion. Hemolysed blood

containing sugars as attractants, results in egg production which is double that obtained from the optimum amino acid mixture. However, if the blood is diluted with water to a total nitrogen level (29 percent blood) equal to that of the amino acid mixture, egg production drops to approximately one-tenth of that of the amino acids. Thus, at an equivalent nitrogen level, blood is a poor medium for egg production as compared to amino acid mixtures. Low solubilities of some of the amino acids prevent raising the nitrogen level of mixtures of these materials to equal undiluted blood.

Discussion: One is immediately impressed with the similarity between the qualitative amino acid requirements of the adult mosquito for egg production and the requirements which have been determined for growth in various organisms. Perhaps of greater significance is the fact that the same amino acids have been reported to be required for growth of the larval mosquito as have now been determined for egg production. The only deviation between the two studies is in the position of glycine which is apparently required by the larvae.

These similarities in amino acid requirements also extend to the quantitative requirements among various organisms. For example, phenylalanine always seems to be required in large amounts, whereas, acids such as threonine and tryptophane are adequately supplied in smaller quantities. Similarities between the nutritional requirements of the mosquito for egg production and other organisms for growth and nitrogen maintenance also exist in their abilities to utilize the D isomers of certain amino acids and in the interrelationships they show between the acids involved in the ornithine cycle.

That the same amino acids appear to be required for both growth and egg production in the mosquito is certainly not surprising, and the same relationship may hold true generally for other organisms. Indeed, it is conceivable that the present work could serve as a basis for assuming that the relationship is true in animals in which it is impossible to separate the needs for reproduction from other metabolic needs, and thereby, probably impossible to determine these needs. This study also serves to illustrate the amino acid requirements of an organism which depends solely on blood as a source of dietary protein in the adult stage.

Summary: By feeding chemically defined media to *Aedes aegypti* females, 11 amino acids were found to be essential for a high level of egg production. When arginine, isoleucine, leucine, lysine, phenylalanine, threonine, tryptophane, or valine were omitted from the diet, no eggs were produced. An elimination of histidine, cystine, or methionine resulted in a significant decrease in the number of eggs produced.

Glutamic acid also had a stimulatory effect on egg production, however, this action was apparently due to its contribution of amino groups rather than the remainder of its molecule, and was therefore, not considered essential as an amino acid.

Through comparison with an earlier study on the amino acids required for growth of larval *Aedes aegypti*, it was shown that the amino acid requirements for growth are essentially the same as those for egg production.

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The Frass of Certain Defoliators of Forest Trees in the North Central United States and Canada[1]

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As mentioned by Morris (1942), the forest entomologist is frequently faced with the practical problem of ascertaining the identity of certain insects which have defoliated the trees and disappeared before his arrival. Cast skins and head capsules provide a difficult and uncertain means of identification; and the kinds of damage done by the insects often are alike to such an extent that they are non-specific. There remains the abundant fecal pellet deposit, commonly called frass, which, if studied carefully, is a reliable means of identifying many species.

The earliest reference we have found in the literature pertaining to the examination of larval excrement is in DeGeer (1752). One frass pellet from a species of *Sphinx* was figured and described. DeGeer is also quoted by Eliescu (1932) as having described the pellets of *Lophyrus pini*. In Kirby and Spence (1826), it is stated that " . . . the *excrements* of insects; which, strange as the observation may seem, but it is no less true than strange, are sometimes pleasing to the eye, from their symmetry, and to the taste, from their sweetness. In those that masticate their food they are solid, and in those that take it by suction, fluid or semi-fluid. In the caterpillars of *Lepidoptera* they are of the former description, and every grain wears some resemblance to an insect's egg: as the passage in many of these consists of *six* fleshy parts separated by channels, so the excrement represents six little prisms separated by six channels."

[1]Paper No. 3465, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.

Ratzeburg (1868), in studying the life history of the "Bockkäfer", *Cerambyx dilatatus*, described the passage and characteristics of its larval fecal pellets. In the Judeich and Nitsche revision of Ratzeburg (1895) the fecal pellets of four forest insects are not only described but figured as well in color plates. For example, those of the larvae of the nun moth, *Lymantria monacha* L., are described as short-cylindrical, with six deep longitudinal furrows, and star-shaped in cross-section.

Koch (1928) constructed keys for the determination of insects found on spruce and fir trees, based on the injury they caused in feeding. Incidental to the main text he includes a short description and photographs of the frass of each of six species. During this same year Frost (1928) published a paper on "Insect Scatology" in which he discusses the excrement of insects in its various aspects. He is perhaps the first to make specific mention of the practical value of a study of insect frass (fecula in his terminology), for he suggests its use in determining the presence of insects, their instar and their identification to order and family.

Escherich (1931) states that larval excreta is variously formed and is often characteristic of the individual species. He has photographs of the frass of *Sphinx pinastri* L., *Dendrolinus pini* L., and *Lymantria monacha* L. Eckstein (1939a, 1939b) has called attention to the usefulness of frass for the identification of certain wood-feeding insects. He gives descriptions and dimensions of the frass of the pine beetle, *Myelophilus piniperda* L., and descriptions of the colour, size and composition of the pellets produced by several species of Anobiidae. More recently Hartnack (1943) and Weiss and Boyd (1950, 1952) have contributed to this subject. Hartnack in a section of his book called "Spoorology" has included illustrations of the excrement of a variety of household pests and wood-destroying insects. Weiss and Boyd have described the frass of a considerable number of common leaf-feeding insects and a few other insects with quite different feeding habits. Their descriptions are accompanied by plates of line drawings of the frass pellets.

During the course of an ecological study of the forest tent caterpillar, *Malacosoma disstria* Hbn., Hodson (1941) made a frass examination which included counts of the numbers of pellets, average weight, and linear dimensions. At this time it was noted in agreement with Eliescu (1932) and Nolte (1939) that the pellets from the early stadia of various species are easily confused.

Although the characteristic size, shape, and markings of the fecal pellets were described in some of the earliest books on entomology, these features were not used as tools for specific identification until quite recently. Nolte (1939) published a key to the identification of European species infesting spruce and pine according to their fecal pellets. He observed that difficulties are encountered in such a study because the typical form can be varied by a change in food plants, temperature, humidity, or the presence of poisons. Gösswald (1934) also had noted the effect of environmental factors on the size and weight of the pellets. Nolte was able to separate out certain insects to species while others he was able to take out only as groups. Morris (1942) constructed a key based on texture, shape, and size of frass pellets which he considered to be dependable characters. His key covered 3 families including 14 species of insects that feed on spruce. He suggested making a separate key for the defoliators of each host tree.

Studies of the frass of larvae damaging forest trees have been made to practical advantage in determining the abundance of insects, and in following the course of larval development and survival during outbreaks. The frass drop

has also been used in measuring the success of insecticide treatment. Discussions of the practical use of frass collections are to be found in the papers of Escherich (1914), Schwerdtfeger (1931), Gösswald (1934) and Morris (1949).

In the present study, the object was to differentiate to species as many as possible of the common larvae of defoliating insects found on shade and forest trees. To this end every conceivable fecal pellet character was used even though the distinctions between them were only relative in some species. Even so, it has not been possible to separate out some of the frass much beyond the family; or in other instances two or three species, usually somewhat closely related, had to be removed as a group. In some cases the host species has been used because of the absence of distinctive characters on the pellets. Fifty-seven species representing thirty-nine genera and seventeen families have been treated in this key.

The frass pellets used were collected both from larvae reared in an insectary and from under trees in natural conditions. For many of the species, particularly the sawflies, samples representative of each instar were collected, but in composing the key only the last instar pellets were used. This appears to be the most practical method for not only are the characters most diagnostic in the last instar; but also it is only after the last instar has disappeared that it is necessary to resort to the fecal pellets for identification. Color was used only sparingly because it is so dependent on the particular food plant and the amount of weathering.

In preparing the specimens for preservation and study, we have found it necessary to dry them to keep them free from mold which may make the characters obscure. Also the drying tends to shrink the pellets uniformly and thus make the various striations and furrows more reliable as identifying characters. Our specimens were dried by warming them under a desk lamp for a few hours.

To use the key, it is suggested that a sample of the largest pellets in the collections be examined to avoid fragments and misformed or divided pellets. By using the largest pellets one can also be more sure that the production of last instar larvae is being examined. The photographs in Fig. 1 have been selected to illustrate the characters used in making the principal divisions in the key. They also serve the purpose of illustrating the most common types of frass pellets.

Key to Larval Frass

1. Frass pellets found in webbing on the host tree 2
   Frass pellets found on ground, surface litter or vegetation 9
2. On conifers; pellets mixed with webbing and fragments of needles 3
   On deciduous, broadleaf trees 7
3. Cylindrical; not sculptured or grooved 4
   Irregular form; surface rough (Fig. 1-A) 5
4. Unbroken pellets less than 3.5 mm. in length; often with broad, shallow, median, transverse constriction ..... *Tetralopha robustella*
   Unbroken pellets over 4.0 mm. in length; without transverse constriction; on pine ..... *Acantholyda zappei*
5. Greatest diameter less than 0.5 mm.; on spruce ..... *Recurvaria piceaella*
   Average diameter more than 1mm. 6
6. On balsam fir or spruce ..... *Choristoneura fumiferana*
   On jack pine ..... *Choristoneura pinus*
7. Length about 2 mm. (Fig. 1-A) ..... *Malacosoma americana*
   Length 1 mm. or less 8
8. On oak ..... *Archips fervidana*
   On cherry ..... *Archips cerasivorana*

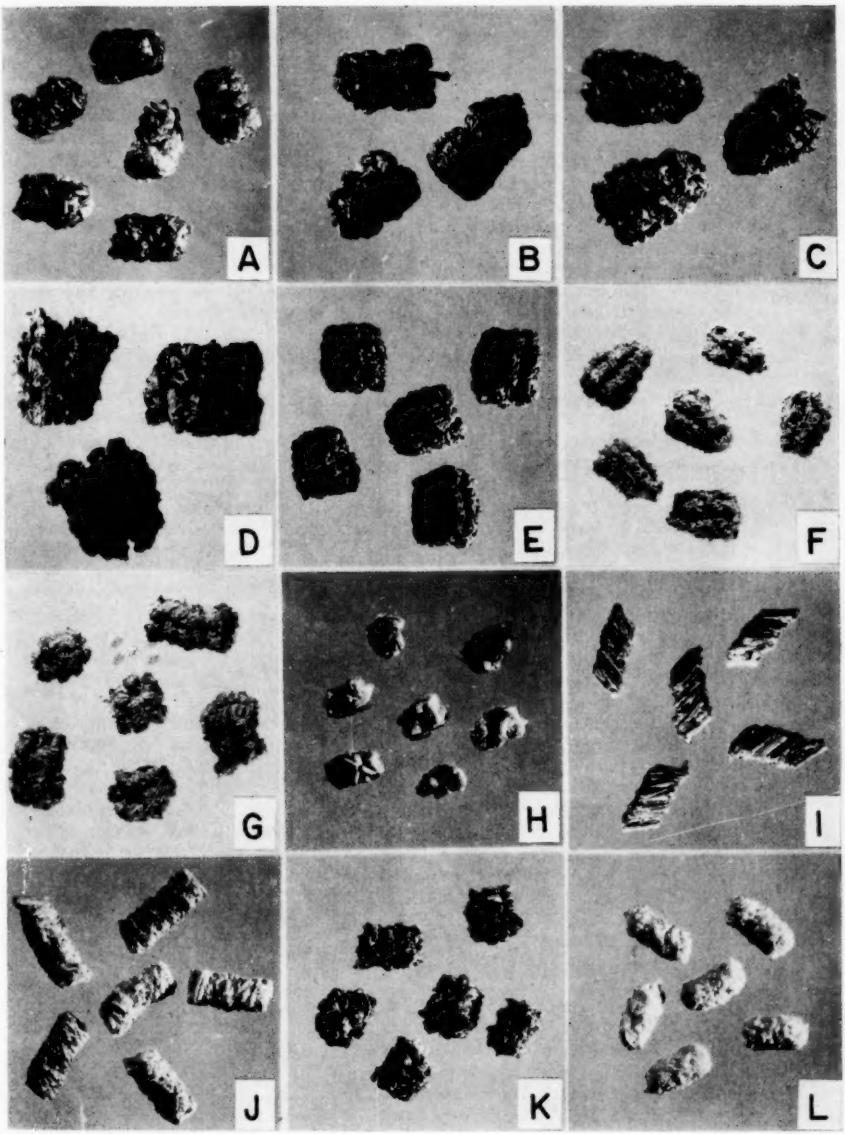

Figure 1. Frass pellets (approximately 4.75X)
A. *Malacosoma americana*, B. *Acronycta americana*, C. *Anisota virginiensis*, D. *Automeris io*, E. *Anisota rubicunda*, F. *Datana integerrima*, G. *Nymphalis antiopa*, H. *Lambdina fiscellaria*, I. *Diprion similis*, J. *Neodiprion lecontei*, K.*Anomogyna elimata*, L. *Pikonema alaskensis*.

9. Elongate, length about 4 to 5 times diameter; pellet much twisted ..... *Diapheromera femorata*
Length usually less than 3 times diameter 10
10. Cylindrical or spherical with six longitudinal grooves or with transverse constrictions (Fig. 1-C and Fig. 1-B) 11
Form various, without distinct grooves or constrictions (spaces between parallel needle fragments not considered grooves) 26
11. With transverse constrictions (single discs may become separated); color brownish-black ..... *Vanessa atalanta*
With longitudinal grooves 12
12. Truncate at one end, tapering to bluntly rounded opposite end (if variable, at least some specimens tapering); greatest dimension less than 3.5 mm. (Fig. 1-C) 13
Usually truncate at both ends; greatest dimension more than 3.5 mm. (Fig. 1-D) 17
13. Average length over 3 mm. 14
Average length 3 mm. or less (Notodontidae and Ceratocampidae) 16
14. Median, longitudinal striae on ridges distinct; form variable, may be truncate at both ends or tapering to bluntly rounded opposite end; on maple (Fig. 1-E) ..... *Anisota rubicunda*
Median, longitudinal striae, if present, indistinct; form consistently tapering from larger truncate end 15
15. Average length over 3.5 mm.; on oak (Fig. 1-C) ..... *Anisota senatoria*
Anisota virginiensis
Average length less than 3.5 mm.; more commonly on other hardwoods ..... *Datana ministra*
16. Conspicuous small fibers projecting from among plant fragments; on walunt (Fig. 1-F) ..... *Datana integerrima*
No conspicuous small fibres projecting, on other species of deciduous trees.
Principally on oak, basswood, birch, and beech ..... *Heterocampa manteo*
Principally on oak, basswood, and birch ..... *Symmerista albifrons*
Principally on elm and birch ..... *Heterocampa bilineata*
Principally on apple, willow, poplar, cherry, and elm ..... *Schizura concinna*
17. Very large, average diameter more than 3.5 mm. (Saturniidae) (Fig. 1-D) 18
Smaller, average diameter less than 3 mm. 21
18. Longitudinal ridges with roughly sculptured surface; coarse plant fragments sometimes interrupting or completely obscuring the longitudinal grooves; pellets of nearly uniform diameter throughout length 19
Longitudinal ridges generally uniform; plant fragments generally fine and embedded in matrix; longitudinal grooves distinct; most pellets taper slightly to somewhat rounded end 20
19. Pellets 5.0 to 8.0 mm. in length ..... *Samia cecropia*
Pellets less than 5.0 mm. in length (Fig. 1-D) ..... *Automeris io*
20. Longitudinal ridges with median striae; surface of ridges often broken by transverse striae into regular blocks ..... *Telea polyphemus*
Longitudinal ridges usually without median striae; transverse striae usually absent; surface of ridges not divided into blocks ..... *Tropaea luna*
21. Length and diameter about equal 22
Length greater than diameter 23
22. Longitudinal grooves deep and narrow; median, longitudinal striae present on ridges; on oak ..... *Anisota stigma*
Longitudinal grooves indistinct and shallow; no median, longitudinal striae on ridges; on elm, poplar, and other deciduous trees ..... *Hemerocampa leucostigma*
23. Cup-like depression at one or both ends of pellets (Fig. 1-G) 24
No cup-like depression at ends of pellets 25
24. Average length about 3 mm.; grooves open (Fig. 1-G) ..... *Nymphalis antiopa*
Average length less than 2.5 mm.; grooves closed ..... *Polygonia interrogationis*
25. Longitudinal grooves distinct; one conspicuous transverse constriction may be present (Fig. 1-B) ..... *Acronycta americana*
Longitudinal grooves indistinct; transverse constrictions, when present, two in number ..... *Notolophus antiqua*
26. On deciduous, broadleaf trees 27
On conifers; in most cases needle fragments evident in pellets 34
27. Length at least 2 times diameter; color black, often with white stripes or spots ..... *Arge pectoralis*
Length less than 2 times diameter 28

28. Average length more than 2 mm. 29
Average length about 1 mm. 33
29. Plant fragments small, embedded in matrix to form relativley smooth surface ..... *Hyphantria textor*
Plant fragments coarse, giving pellets rugose apearance 30
30. Cylindrical form quite regular 31
Cylindrical to subspherical; rough surface tends to obscure regular geometrical form 32
31. Principally on poplar and willow ..... *Basilarchia archippus*
Principally on basswood and cherry ..... *Basilarchia arthemis*
32. On poplar, oak, and maple ..... *Malacosoma disstria*
On cherry and apple (Fig. 1-A) ..... *Malacosoma americana*
33. Surface uniformly and finely rugose; ends usually rounded or truncate without cup-like depressions; color shiny black; on ash ..... *Tomostethus multicinctus*
Surface uneven; cup-like depressions often present at one or both ends; on several species of deciduous trees (Geometridae) ..... *Alsophila pometaria*
Paleacrita vernata
Ennomos subsignarius
34. Needle fragments held together loosely and without any regular arrangement; no cementing matrix filling spaces between fragments (Geometridae) Fig. 1-H) 35
Needle fragments bound together in a matrix; with or without an orderly arrangement of the fragments 36
35. Average length 2 mm. or more (Fig. 1-H) ..... *Lambdina fiscellaria*
Average length less than 2 mm. ..... *Nepytia canosaria*
36. Rhomboidal, rectangular, or trapezoidal, with both ends cut off sharply; needle fragments not small and buried in matrix, usually arranged in diagonal and parallel rows (Diprionidae) (Fig. 1-I) 37
Form variable, cylindrical to subspherical, one end may be cut off sharply; needle fragments mostly embedded in matrix, never arranged regularly in parallel rows (Tenthredinidae and Agrotidae) (Fig. 1-L) 43
37. On balsam fir and spruce; frequently curved or twisted 38
On species of pine 39
38. Principally on balsam fir; form rhomboidal; needle fragments generally arranged in parallel rows ..... *Neodiprion abietis*
Principally on spruce; form variable, rhomboidal to subcylindrical; needle fragments not distinctly parallel ..... *Diprion hercyniae*
39. Principally on white pine 40
Principally on red, jack, and Scotch pine 41
40. Form uniformly rhomboidal; length about 3 to 3.5 mm. (Fig. 1-I) ..... *Diprion similis*
Form variable, rectangular to rhomboidal; length 2 to 2.5 mm. ..... *Neodiprion pinetum*
41. Larvae feed only on old needles ..... *Neodiprion virginianus*
Neodiprion nanulus
Neodiprion pratti banksianae
Larvae feed on both new and old needles 42
42. Form uniformly rhomboidal; sides very flat; needle fragments arranged in consistently parallel rows; their edges raised to produce a corrugated surface; on red and Scotch pine ..... *Diprion frutetorum*
Form variable, from rectangular to trapezoidal; sides not distinctly flattened; needle fragments often do not extend full width of pellet and are partially buried in matrix; on red and pack pine (Fig. 1-J) ..... *Neodiprion lecontei*
43. Form variable but tends toward subspherical; about 1 mm. in length; small plant fragments (not needles) embedded in matrix; on northern white cedar and juniper ..... *Monoctenus melliceps*
More than 1 mm. in length; plant fragments recognizable as needles; principally on tamarack, spruce, or pine 44
44. Length over 2 mm. and 2 to 3 times diameter 45
Length less than 2 mm. 46
45. On spruce and pine; needle fragments relatively coarse and curled ..... *Pamphiliidae*
On tamarack; pellet compressed to form relatively smooth surface ..... *Pristiphora erichsonii*
46. Broad and shallow transverse constriction usually present; sometimes a depression at one end (Fig. 1-K) 47
Without transverse constriction or terminal depression 48
47. Terminal depression a shallow concavity (Fig. 1-K) ..... *Anomogyna elimata*
Terminal depression minute or absent ..... *Feralia jocosa*

48. Color brown when dry; on tamarack ..... *Anoplonyx luteipes*
Color tan; on spruce (Fig. 1-L) ..... *Pikonema alaskensis*
Pikonema dimmockii

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Phygadeuon trichops Thoms. (Hymenoptera: Ichneumonidae), an Occasional Parasite of *Hylemya* spp. (Diptera: Anthomyiidae)[1]

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In extensive surveys for parasites of *Hylemya brassicae* (Bouché), *H. floralis* (Fall.), and *H. cilicrura* (Rond.) on cruciferous crops in Canada and Europe, observations were made on the life-histories and behaviour of the parasites. Accounts of the two most abundant parasites, *Aleochara bilineata* Gyll. and *Trybliographa rapae* (Westw.), have already been published, the former by Colhoun (1953) and the latter by Wishart and Monteith (1954). The present paper deals with one of the minor parasites, *Phygadeuon trichops* Thoms. In the surveys this parasite was found in Norway, Holland, and Scotland but in such small numbers as to indicate that it has other, preferred hosts and that it only occasionally attacks *Hylemya* spp. *Phygadeuon fumator* (Grav.) was reared from *Hylemya* sp. from France and is recorded in the literature from *Hylemya* spp. in Russia (Meier, 1927; Vodinskaya, 1928) and in England (Wadsworth, 1915). No references were found to *P. trichops* from *Hylemya* spp. and no accounts of the biology of either species.

Specimens of *P. trichops* used in this study were identified by Dr. Wm. R. M. Mason, Entomology Division, Ottawa, from a culture established from individuals reared from hosts collected in Norway. Dr. Mason also identified specimens from Holland and Scotland as *P. trichops*. Dr. Ch. Ferriere, Geneva, Switzerland identified specimens from Scotland as *P. trichops* and from France as *P. fumator*.

Materials and Methods

Breeding stocks of the parasites were maintained in the laboratory in screen-covered cages 18 inches high, 12 inches wide, and 10 inches deep, with wooden frames and bottoms, and sliding fronts made of acrylic resin sheeting.

Several methods were employed to expose host puparia for oviposition. Female parasites attacked puparia lying loose on the bottom of the cage but did so more readily if the puparia were prevented from rolling. Puparia placed on corrugated paper were attacked but many of the females hid in the partially closed parts of the paper. The most satisfactory medium was a thin layer of fine gravel (bird gravel). This made the puparia accessible to the females and the puparia were removed easily from the gravel by sifting through a screen. Each parasitized puparium was placed in a one-inch shell vial closed by a stopper made of fine-mesh nylon and a small piece of latex tubing, as described by Colhoun (loc. cit.). During development the vials were kept in a room at 74-76°F. and 60 per cent relative humidity. Observations on the numbers of eggs laid, hatching, and subsequent development were made without opening the puparia; a binocular microscope was used with strong light while the puparia were submerged in water or moistened with a brush. Observations on the number of instars were made by carefully dissecting hundreds of host puparia at intervals during larval development.

Descriptions of Immature Stages

Egg

The egg of *P. trichops* (Fig. 1) is ovoid with both ends smoothly rounded. The average length is 0.75 mm. and the width 0.21 mm. It is opaque white; the chorion is smooth throughout.

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Larva

There are five larval instars. The head is distinct from the thirteen body segments. There are nine pairs of open spiracles in each instar. One pair is situated on the posterior margin of the first thoracic segment and the others on the anterior margins of the first eight abdominal segments. The cephalic structures (Figs. 2 to 6) are well defined, sclerotization being more pronounced in the later instars.

The average measurements in millimetres of the five instars are as follows:

	1st	2nd	3rd	4th	5th
Length	0.88	1.37	2.60	4.35	5.6
Width	0.35	0.58	1.20	1.80	2.6

Prepupa and Pupa

The prepupa is 5.20 mm. long and 2.5 mm. wide. It is slightly smaller than the ultimate larval instar and has no features that differ significantly from prepupae of other parasitic Hymenoptera. The imaginal eyes are visible.

The pupa is approximately the same size as the prepupa. A silken cocoon completely encloses the pupa within the host puparium. This is an exception; Clausen (1940) states that hymenopterous parasites do not spin cocoons in dipterous puparia. The exuviae of the five larval instars are attached to the cocoon.

Reproductive Systems

Female

The female reproductive organs (Fig. 7) are of the ichneumonoid type as described by Pampel (1914). Each ovary contains five to seven ovarioles that are united anteriorly by terminal filaments. The filaments of the two ovaries are joined dorsad of the alimentary canal. The ovaries are polytrophic, each containing three or four eggs of which only one is mature. Short oviducts connect the ovaries to the common genital duct. The spermatheca is a minute saclike organ situated on the median dorsal anterior surface of the genital duct. The alkaline gland is unbranched and opens into the vagina slightly anterior to the terebra. The poison sac is connected to the vagina near the opening of the alkaline gland by a long duct. Attached to this duct and the poison sac is the branched acid gland.

Male

The reproductive organs of the male (Fig. 8) are simple. The single median organ contains the paired testes enclosed in a scrotal membrane. The paired vasa deferentia, with a vesicula seminalis attached to each vas deferens, unite in a common ejaculatory duct which opens into the aedeagus.

Development

Behaviour of Adults

Both sexes are active immediately after emergence; the females often gnawed through the cloth stoppers and escaped from the vials in the laboratory. The response to light of both males and females is not marked; they hide, however, beneath or behind objects used for feeding or oviposition. The adults have an average longevity of 29.5 days, the females usually living slightly longer than the males.

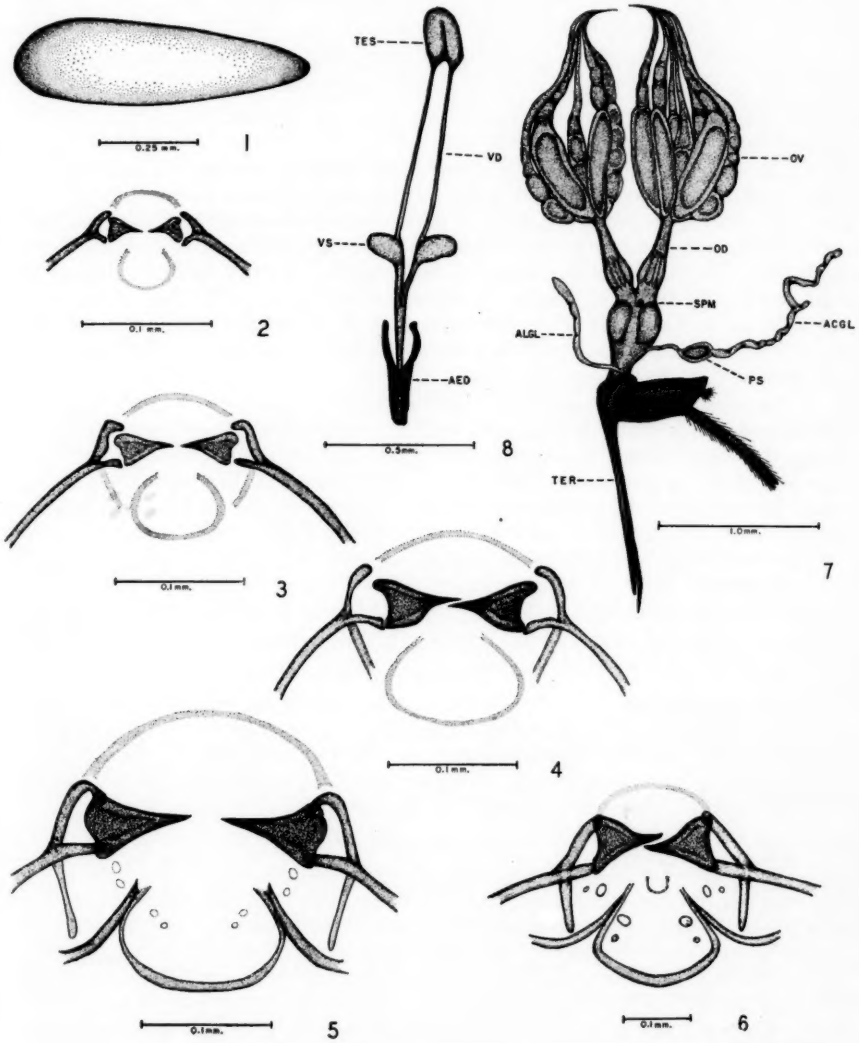
Mating

Copulation may take place immediately after the adults have emerged. It requires 25 to 40 seconds and occurs at any temperature at which the parasites are normally active. No prolonged courtship precedes the act of copulation. The males move about excitedly, waving their antennae and fluttering their

wings when a female is near. Mating is almost certain to take place if the female is stationary or moves slowly. Females were observed to mate more than once.

Oogenesis and Oviposition

Females sometimes oviposited within a few hours after emergence but the average preoviposition period was three days. Oviposition occurred freely on



Figs. 1-8. *Phygadeuon trichops* Thoms. 1, Egg. 2-6, Mandibles; 2, first-instar larva; 3, second-instar larva; 4, third-instar larva; 5, fourth-instar larva; 6, fifth-instar larva. 7, Reproductive organs, female; ACGL, acid gland; ALGL, alkaline gland; OD, oviduct; OV, ovary; PS, poison sac; SPM, spermatheca; TER, terebra. 8, Reproductive organs, male; AED, aedeagus; TES, testes; VD, vas deferens; VS, vesicula seminalis.

H. brassicae, *H. floralis*, *H. cilicrura*, and *H. antiqua* Mg. The deposition of an egg required five to 21 minutes. The average period over which eggs were laid was 18.3 days; females lived an average of 8.5 days after laying their complement of eggs. The average number of eggs per female was 47.9 with a maximum of 72 from one female. Eggs were deposited on the pupa within the host puparium and were found on all parts of the host, most commonly on the dorsum between the thorax and abdomen. Females did not discriminate between puparia already containing eggs and those without any. The greatest number of eggs found in one puparium was 15, two to six being found often.

At 74-76°F. hatching occurred two to three days after the eggs were laid. The larva, which lies extended within the egg, frees itself by using its mandibles.

Larval Development

The development of the larva was easily studied through the walls of the host puparium. The first-instar larva becomes active immediately after leaving the egg and moves freely within the puparium. Subsequent instars move only to establish new feeding points. Feeding is completed during the fourth larval stadium. The fifth, or ultimate, larval instar spins a cocoon, voids its meconium, and eventually pupates. Slight variations were observed in the duration of each larval stadium. The first and second stadia each appeared to require two days, the third and fourth each approximately one day, and the fifth, including the prepupa, 12 to 13 days.

The gut is blind during larval development and remains so until after the ultimate instar forms a cocoon and orients itself in the same direction as the host; then the meconium is voided. The exoskeleton of the host and all larval exuviae are attached to the cocoon. Parasitized puparia are always darker than those that are unparasitized, some being almost black. This discolouration is first observed after the cocoon is formed. Wadsworth (1915) reported similar discolouration of an *H. brassicae* puparium from which he obtained a female of *P. fumator*.

There is no diapause but, at a temperature of 45°F., development is arrested during the ultimate instar. This occurs after the cocoon is formed but before the meconium is voided.

Emergence of Adults

The adult emerges by gnawing an irregular hole through the host puparium, usually in the anterior region. Males are the first to emerge. The average developmental period from egg to adult was 20.1 days, 19.6 for males and 20.6 for females. Most emerged during the early morning hours.

Superparasitism

Whether more than one egg is deposited in a single host in the field is not known, but in the laboratory superparasitism was the rule rather than the exception. Supernumerary parasites were always eliminated; in no instance did more than one parasite complete development in a host. Where one egg hatched before the others, the larva destroyed the other eggs with its mandibles. Where the eggs hatched about the same time, two or more larvae co-existed for a short time; in a few hosts more than one larva was present until the third or fourth instar. In the majority of hosts, elimination of supernumerary parasites occurred before the second instar, when the first larva to hatch was the more active. All that remained of the destroyed larva was the cephalic structures. The presence of supernumerary larvae did not appear to alter the rate of development or size of the surviving parasite.

Overwintering and Effects of Low Temperature

Several generations of *P. trichops* were reared in the laboratory with uninterrupted development. It is assumed therefore that this species is homodynamic (Roubaud, 1922).

Parasites collected in the field in October were in the ultimate larval instar. After several months at 45°F. there was no evidence of further development and the meconia were not cast. It is therefore assumed that the winter is passed in this stage. The threshold of development was not determined but it was established that although development occurred at 45°F. it progressed to the adult only under certain conditions. Parasites placed at 45°F. after development at 74-76°F. for less than eight days developed at a reduced rate to the ultimate instar. At this stage development ceased but was resumed when the parasites were exposed to higher temperatures. However, if they were allowed to develop at 74-76°F. for more than eight days and were then transferred to 45°F., development proceeded slowly until ultimately the adults emerged. It is obvious that the effects of temperatures below 45°F. were different on young larvae from those on older ones. Parasites exposed to low temperatures, whether young or old, resumed normal development when brought to room temperature. The insect cannot, therefore, have a true diapause in the sense used by Shelford (1929) because there was no evidence of changes taking place of a physico-chemical nature.

Summary

Phygadeuon trichops Thoms., which is widely distributed in Europe attacks *Hylemya* spp. only occasionally. Females deposit their eggs on the host pupa within the puparium. They do not discriminate between parasitized and unparasitized puparia in the laboratory; superparasitism is common but only one parasite survives. There are five larval instars, which require nine to 10 days for development to pupation. Development from egg to adult requires about 20 days. The ultimate instar forms a cocoon within the host puparium. The insect does not have a true diapause but overwinters in the last larval stage within the cocoon.

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The Genus *Orenaia* in North America, with the Description of a New Species (Lepidoptera: Pyralidae)[1]

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The most recent list of the North American species of *Orenaia* was given by McDunnough (1939: 14), who referred two species to the genus. In the present paper two nominal species are transferred from *Titanio* to *Orenaia*, one as a synonym, and a new species of *Orenaia* is described.

Titanio and *Orenaia* agree in the reduced eyes, stout build, hairy vestiture, and noctuid-like facies. However, as was first shown by Müller-Rutz (1929), the genitalia of *Orenaia* are indistinguishable from those of *Evergestis*, whereas those of *Titanio* are of a very different type. The similarity in habitus of the two genera is undoubtedly the result of convergence.

Hampson (1899) distinguished *Titanio* from *Orenaia* by the vestiture of the labial palpus, in *Titanio* the third joint being concealed by long, hair-like scales arising from the second joint, whereas in *Orenaia* it is exposed. The superficial nature of this difference is shown by the fact that it led Barnes and McDunnough to place the male of a species in *Titanio* and the more smoothly scaled female in *Orenaia*. A more reliable difference is found in the sclerites of the labial palpus, *Orenaia* having the first joint as long as the second, whereas *Titanio* and related genera have the first joint much shorter than the second. The male genitalia of *Orenaia* have the uncus pointed and the valve simple, as in *Evergestis*, whereas those of *Titanio* have the uncus bilobed and the valve radially striated.

The points distinguishing *Orenaia* from *Evergestis* are less definite and less fundamental. *Orenaia* has a stout, noctuid-like build, bushy vestiture, and reduced eyes, partly or wholly surrounded by a scaleless zone. In *Evergestis* the build is slender, the vestiture is moderately to very smooth, and the eyes are not reduced, all the bordering sclerites except the gena being scaled. Hampson describes the frons as rounded in *Orenaia* and as flat and oblique in *Evergestis*, but both configurations exist in each genus.

Orenaia trivialis Barnes and McDunnough

Figs. 1, 2, 4

Orenaia trivialis Barnes and McDunnough, 1914: 236, Pl. 1, Fig. 13.
Titanio subargentalis Barnes and McDunnough, 1918: 161. New synonymy.

Barnes and McDunnough's figure is adequate, and represents a specimen intermediate between the extremes of variation. In strongly marked specimens the antemedial, postmedial, and subterminal bands are all well marked, black, of irregular width, and defined inwardly by conspicuous bands of silvery-grey scales. There is a definite, silvery-grey reniform spot, and two black spots in the basal area. At the opposite extreme of variation are specimens with no silvery-grey scaling whatever on the fore wing, and with the dark bands reduced; in these there are always at least a dark reniform ring-spot and a postmedial band, both of them obscure.

The palpi of the male are densely hairy; those of the female are clothed with short hairs and long scales, arranged in a more or less smooth vestiture. This sexual difference led Barnes and McDunnough to place the male and female in different genera. The genitalia are of the *Evergestis* type. The male genitalia

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are in general similar to those of the following species, in the description of which the diagnostic differences are pointed out.

Material examined: The types, and 9 males, 5 females, from: Flat-top Mt., Rocky Mountain National Park, Colo.; Moraine Lake, Alta.; Mt. McLean and

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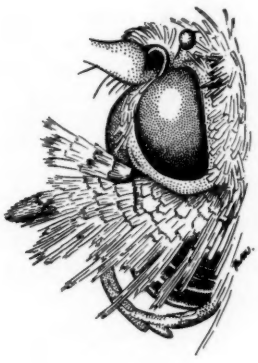

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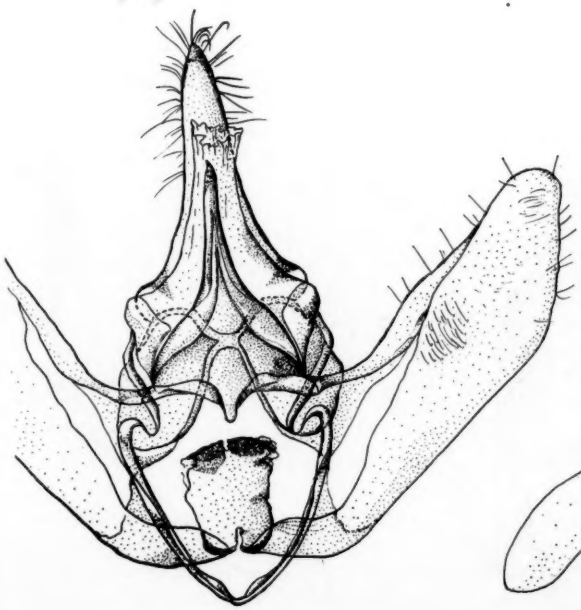

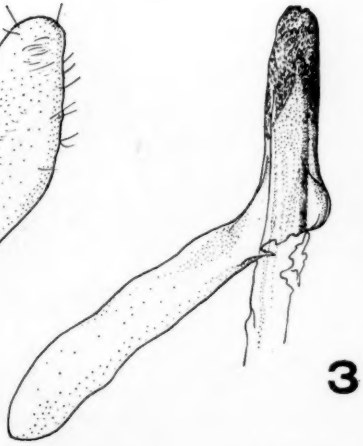

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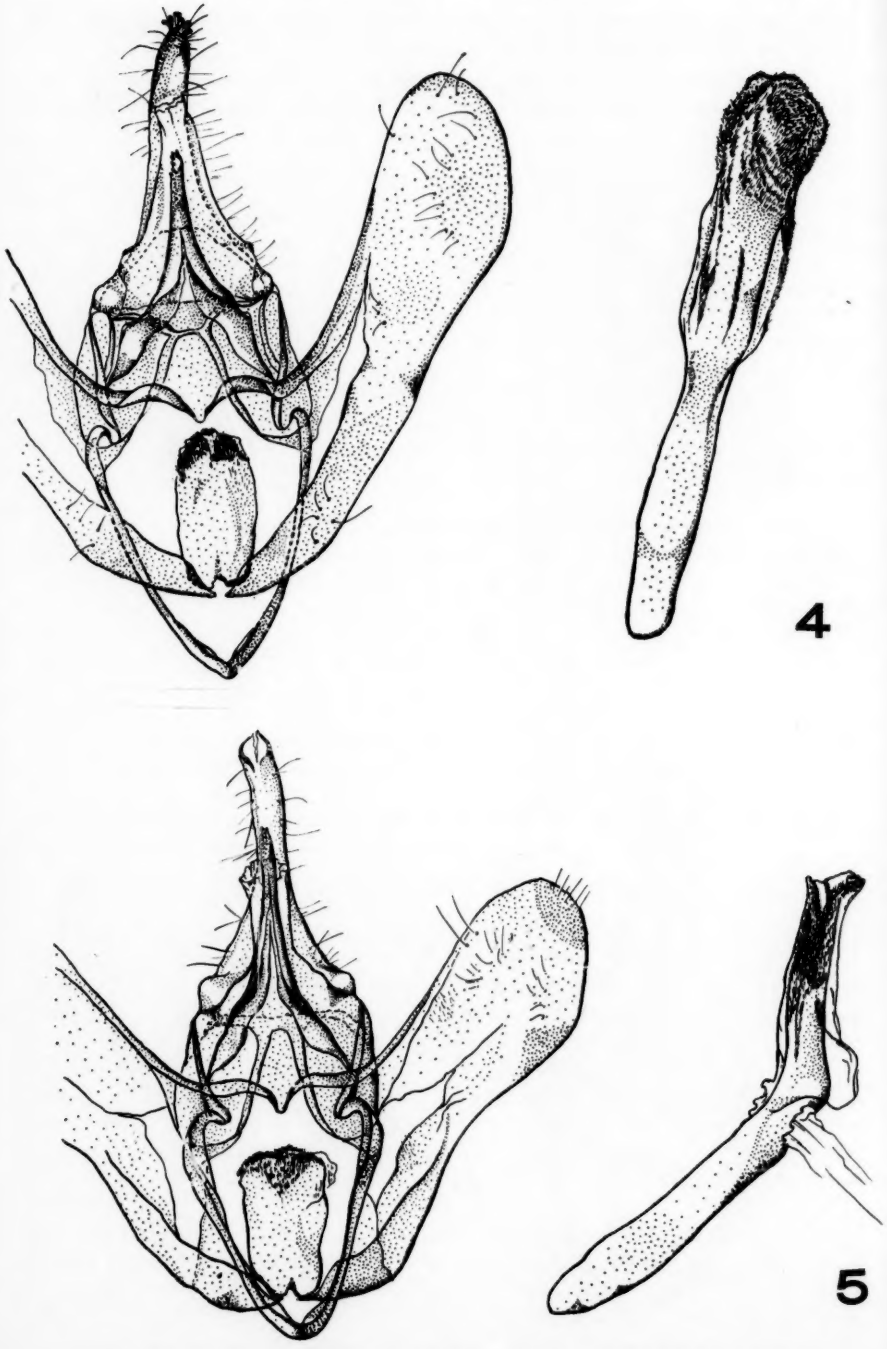
Figs. 1-3.—1, *Orenaia trivialis*, ♂, head; 2, *Orenaia trivialis*, ♀, head; 3. *Orenaia pallidivittalis*, ♂, genitalia.



Figs. 4-5.—4, *Orenaia trivialis*, ♂, genitalia; 5, *Orenaia coloradalis*, ♂, genitalia.

Lillooet district, B.C.; Jesmond, B.C. All the specimens were taken in July, and the altitudes recorded are from 6000 to 7500 feet .

***Orenaia pallidivittalis*, new species**

Figs. 3, 6

Male. Head, thorax, and dorsum of abdomen dark brown, a few pale-brown scales in collar and anal tuft. Palpi densely clothed with long bushy hairs. Abdomen pale brown below. Legs brown, outer surfaces of femora and tarsi dark brown. Fore wing dark brown, dusted with pale-brown scales, most heavily along the middle third of the costa. Antemedial line dark, very obscure, almost erect; postmedial line dark, narrow, outwardly oblique behind costa. then bent abruptly to become slightly oblique inward beyond the cell, gradually incurved behind cell to below reniform, then erect to the inner margin. Reniform oval, preceded by a definite, oval, pale-brown patch and followed by a similar patch,

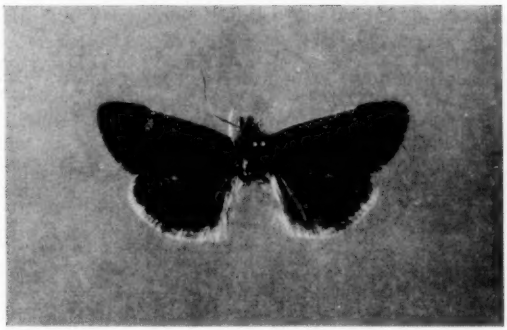


Fig. 6.—*Orenaia pallidivittalis*, holotype ♂, ×2.

the two patches resembling at first sight pale reniform and orbicular spots. Fringe dark brown, an interrupted darker line near its base. Hind wing dull brown, paler near costa, with a very obscure, evenly curved, postmedial line. Fringe paler than that of fore wing, otherwise similar. Under side of wings pale brown. Fore wing with a definite reniform lunule, outlined in dark brown; fore and hind wings with evenly curved, dark, postmedial and terminal lines. The paratype has the whole area beyond the postmedial line dark brown. Fringes basically pale brown with a dark medial line. The holotype has the distal half of the fringe of the fore wing dark; the paratype has the entire fringe of the fore wing, and the basal half of the fringe of the hind wing, dark.

Male genitalia similar in general structure to those of *O. trivialis*, differing in the following respects: apex of uncus more strongly acute; gnathos proportionally shorter; aedoeagus more slender; valve not expanded before apex.

Female unknown.

Holotype, male, and one male paratype: Mount Stephen, B.C., ca. 7000 ft.; July 7, 1917; F. H. Wolley-Dod. Type No. 5945, C.N.C.

This species is closest in appearance to *Titanio alticolalis* Barnes and McDonnough, which, though I have not been able to examine it structurally, probably falls in the present genus. *O. pallidivittalis* differs in having the costa much less highly arched at the base, in the presence of two well-defined pale spots on the disc of the fore wing, and in the much longer and more prominent reniform spot on the under side.

***Orenaia coloradalis* Barnes and McDunnough**

Fig. 5

Orenaia coloradalis Barnes and McDunnough, 1914: 236, Pl. 1, Fig. 13.
Titanio species 1, Gibson, 1920: 45.

Barnes and McDunnough's description and figure are adequate. Dyar and Gibson were unable to recognize the Canadian Arctic Expedition specimens because of poor condition. Fresher specimens agree well with the type, and show that the species is widely distributed, though rare.

In addition to the type, from Colorado, I have examined the two specimens recorded by Gibson from Bernard Harbour, N.W.T., one male from Repulse Bay, N.W.T., and one male and one female from Eskimo Point, N.W.T.

Acknowledgments

The figures of heads were drawn by Miss M. R. MacKay, and those of genitalia by Miss M. d'Aoust, Insect Systematics and Biological Control Unit, Ottawa.

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A Note on the Occurence in Canada of the Purse-Web Spider, *Atypus niger* Hentz. (Araneae: Atypidae)

By DONALD P. GRAY*

In June, 1955, a spider collected at Harrow, Ontario, May 28, 1955, by Mr. Robert Walsh of the Science Service Laboratory there, was sent to the author for determination. This specimen proved to be a mature male of the species, *Atypus niger* Hentz, commonly known as a "Purse-Web" spider. Subsequently, Dr. Willis J. Gertsch, of the American Museum of Natural History informed me that several years ago he determined a female of *Atypus niger* found at Grimsby, Ontario (1). This specimen was collected on July 12, 1942, by Wm. L. Putman, of the Science Service Laboratory, Vineland, Ontario. Apparently Mr. Putman's specimen represents the first of this species to be taken in Canada. I am indebted to Dr. Gertsch for his kindness in making this information available for use at this time.

The suborder Mygalomorphae, of which *A. niger* is the only representative to be found in this region, includes the so-called "tarantulas" and their allies. Most members of this group are found in the warmer regions of the world.

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In the Mygalomorphae, the chelicerae project forward in front of the cephalothorax, and each fang is directed caudally, roughly parallel with the long axis of the body (paraxial articulation). All spiders heretofore known from Canada have the chelicerae articulated so that the fangs move in a transverse plane to the long axis (diaxial articulation).

A brief summary of the characteristics of the family Atypidae would include, in addition to paraxial chelicerae, 2 pairs of lung books, eight eyes with the anterior median eyes alone dark, six spinnerets, three pairs of cardiac ostia, anal tubercle situated some distance above the posterior spinnerets, and well developed endites.

Spiders of the genus *Atypus* are of some interest because of the curious manner in which they capture their prey.The spider lives in an excavation in the ground. The silken lining of the burrow is continued above the surface to form a cylindrical web roughly a foot in height. The cylinder is generally camouflaged with bits of moss, tree bark, sand, etc. to blend in with the background. The usual practice is to lean the cylinder against a tree trunk or other support. When complete, the tube is attached at its upper extremity to the support, and the whole is tautly stretched. The vibration caused by an insect landing on the outside of the tube is transmitted to the spider lurking below in its burrow. It rushes up inside the tube and impales its victim through the web by means of its chelicerae. The prey is then pulled in through a slit opened in the tube, and is consumed. After completion of the meal, the remains are ejected from the web, and the rent is repaired. An excellent plate, in colour, showing the snare is presented by Gertsch (2).

After reaching sexual maturity, *Atypus* males leave their snares and wander about seeking out the sedentary females. It is at this time that most of these spiders are noticed, which probably accounts for the predominance of male specimens in collections.

Poteat (3) has written of the habits of *Atypus niger*, and Bishop (4) of those of the related *A. abbotii* (Walck.), and it is probable that the other members of the genus exhibit comparable behaviour.

A. niger has been recorded previously from the northeastern part of the U.S., from Massachusetts and Connecticut westward into Wisconsin and Michigan. According to Gertsch (1) it is nowhere common, as only one or two individuals a year fall into the hands of collectors.

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Studies of Parasite Oviposition Behaviour. I. *Mastrus carpocapsae* Cushman. (Hymenoptera: Ichneumonidae)

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Introduction

The oviposition behaviour of numerous parasites toward hosts already parasitized has been the subject of a considerable number of investigations during the past twenty years. Many species of ichneumonids, braconids and chalcids have been shown generally to avoid oviposition in parasitized hosts under laboratory and field conditions but there are conflicting views on the nature of this behaviour and on the cause for such rejection (Salt 1935, 1937, Ullyett 1936). Incomplete data bearing on these problems with the parasite *Mastrus carpocapsae* are given here. Difficulties in laboratory propagation and particularly irregular and erratic oviposition under the experimental techniques employed have prevented a fuller study; but it is felt that the data will be of interest to workers in this field of behaviour since in certain respects the findings help in the interpretation of relevant facts demonstrated in previous investigations.

Ullyett (1949) proposed a tentative classification of hosts into five major groups for purposes of study of progeny distribution by entomophagous parasites. This grouping was put forward to emphasize the fact that host habits afford variable opportunity for examination of the host prior to oviposition by the parasite. Thus it was postulated that progeny wastage through superparasitism is less likely to occur where the host is a stationary egg of a moth, fully exposed to examination, than in a case where the host is an active larva of the same insect. This viewpoint is a plausible and attractive one, although our present very limited knowledge on superparasitism gives no strong indications that these differences are of great importance in such phases of adult parasite behaviour. It is probably true that a discriminatory faculty is common in the parasitic hymenoptera, and there is evidence that some of the sensory organs involved are located on the antennae, ovipositor and tarsi. From the standpoint of parasite oviposition behaviour and its relation to efficiency of progeny distribution, it would seem advantageous to revise Ullyett's classification of hosts so that greater emphasis is placed on the sensory physiology of the female parasites. All hosts then fall naturally into three groups, those accessible to physical contact by the parasite antennae, tarsi and ovipositor, those which by covering are accessible only for contact by the ovipositor, and finally those never contacted by the adult parasites. Each major group may have subdivisions to include stationary or active hosts.

It is true that separation of the hosts from a parasite by some sort of protective covering may prove to be of little significance in the operation of such sensory receptors as occur in the antennae, tarsi, etc., but the presence of any sort of envelope between the female parasite and the living host is often of importance in the oviposition response and the distribution of progeny. Clausen (1940) has pointed out that many ichneumonids and braconids show little or no interest in their hosts when these are removed from their normal enclosures; Willard's observation (1927) that *Microbracon mellitor* Say, a parasite of the pink bollworm *Pectinophora gossypiella* Saunders, pays attention only to a moving larva within a covering is a specific example. Scattered evidence in the literature shows that there is appreciable variation in regard to actual progeny distribution within such cells. The majority of external parasites attack hosts in protected situations, and many species deposit their eggs as frequently near

the host as on the host, suggesting that the ability to localize the sources of ovipositional stimuli depends on receptors other than those of contact. This form of egg deposition away from the enclosed host reaches an extreme in parasites such as *Tetrastichus xanthops* (Ratz), which develops on larvae of the birch leaf mining sawfly *Phyllotoma nemorata* (Fall). The female apparently pays no attention to the host in the mined leaf, and usually deposits the egg free at the extremity of the mine, from which point the hatched larva crawls to the host. Frequently eggs are laid in mines from which the host larvae have been removed. (Dowden 1941).

Until appropriate data have been amassed, any classification must rest on utilitarian bases. The foregoing remarks illustrate the especially promising field available not only for quantitative investigations of parasite progeny distribution among hosts in protected situations, but also for increasing understanding of perceptual aspects of instinct in parasitic hymenoptera. Baerends (1950), an adherent of the Lorenz school of instinctive behaviour, claims that parasite/prey relations depend on releasing mechanisms adapted to very specific stimuli. There seems more hope of a successful search for these in the behaviour of external parasites.

The parasite chosen for the present experiments is an external attacking protected host-stages. The main objectives were twofold: firstly, to examine again discrimination in an external parasite since Varley (1941) and Andrewartha and Birch (1954) surprisingly imply that this faculty is absent as a rule in such types; and secondly, to test the possibility that any such discrimination between parasitized and unparasitized hosts might be attributed in its initial phases to odour-producing chemical traces left on the host covering etc. by previous ovipositing females as demonstrated by Salt (1937) with *Trichogramma evanescens* West.

Material and Methods

Mastrus carpocapsae is a large species developing as a solitary external on cocooned larvae of the codling moth, *Carpocapsa pomonella* (L.) in California and other sections of North America. Muesebeck et al. (1951) record it as a parasite of *Grapholitha molesta* (Busck) and *Laspeyresia caryana* (Fitch). The salient features of its biology in Southern California are as follows: The parasite is most active on freshly hibernated codling moth on tree trunks etc. during the autumn and early winter months. The host larva is first paralyzed and an egg deposited on any part of the host, or sometimes at any point in the cocoon. At 75°F. oviposition commences 12 to 24 hours after emergence and females lay 3 or 4 eggs daily during a lifetime of 30 days. The egg hatches 36-48 hours after deposition, five larval instars follow in 7-10 days, and the mature larva spins a cocoon within that of the host. Very rarely 2 larvae mature on one host. Most mature larvae remain in this stage throughout the late winter. There is an early spring pupation and some emerging adult parasites oviposit on the more retarded codling moth larvae in the winter cocoons, others on the first summer brood larvae. Most mature parasite larvae on the latter hosts go into diapause in the cocoons during the summer months, and eventually transform in September. This diapause has prevented continuous laboratory production and as an experimental insect this species has been even more unsatisfactory owing to a highly variable sexual maturity in females emerging from hibernating host material. The data reported below refer only to those females which laid during the course of numerous experiments, and on completion of sufficient numbers of these, work with this species was abandoned.

All experiments were done with field material. Hibernating codling moth larvae in cocoons were obtained from Southern California walnut and apple orchards known to be virtually free of parasitism. *M. carpocapsae* adults were used as they emerged from field collections held in the laboratory throughout the fall and winter months. Thus the normal practice of experimenting with mated females of uniform age could not always be followed, but efforts were made to keep age differences to a minimum. Procedure in examining the nature of the oviposition response to various hosts was similar to that outlined in Lloyd (1940). The individual female parasites were maintained for life in glass tubes of 5 inch length and 1 inch diameter, capped by perforated corks surrounded with organdie. Codling moth cocoons from the field collections were sorted so that those used were of reasonably uniform dimensions and construction; they were approximately ¾" long and more or less oval in form. The heavy silk walls are sometimes interwoven with pieces of bark but the surface attaching the structure to the trunk is of lighter texture, which facilitates slitting to change the cocoon contents. Cocoons were lightly gummed by this weaker surface at ½" intervals on strips of stiff drawing paper. Groups of six cocoons were alternated in the manner U P U P U P, where U represents unparasitized hosts and P parasitized ones. In the present series of experiments these hosts were exposed to the tubed individual females for eight hours at a constant temperature of 75°F. and relative humidity of 50 to 60% under normal daylight.

The oviposition behaviour:

The female after preliminary antennal examination mounts the cocoon and probes with the ovipositor until an entry is effected, the contained host being located and stung with one quick thrust. Active codling moth larvae removed from the cocoons received no attention, a fact in accord with the opinion of Thorpe (1950) that perception of temporal and spatial relations is, in some infinitesimal measure, inherent in all animal receptor activities and responses. Paralysis is rapid and the female may withdraw her ovipositor or wait with it in the cocoon. McClure (1933) states that the egg is laid at the point of stinging but the finding of eggs at any point within the cocoons indicates flexibility in this respect. Host paralysis often occurs without subsequent oviposition (Flanders 1926), but no host feeding has been reported by earlier workers and none was noted in the current work. Ullyett (1949-1950) considered that at least under laboratory conditions *Microbracon hebetor* Say and *Cryptus inornatus* Pratt searched the micro-environment in two phases, first paralyzing all the hosts in the immediate vicinity and then relocating them to oviposit. No firm conclusion on this unusually interesting type of behaviour could be drawn from observations on *Mastrus*, and difficulties in securing females of uniform sexual maturity may have obscured any tendencies to pronounced temporal sequences in paralysis and oviposition in this species.

To test discrimination between unparasitized and parasitized hosts, assess the nature of such rejection, and generally examine its bearing on the problem of host perception by the parasite, series of hosts given below were set up. A conditioned cocoon was one from a codling moth larva which had been paralyzed and oviposited on within two hours previous to use in the experiments. Unconditioned cocoons were those which had not been touched by female parasites before use in the experiment tubes. Coddled host larvae were those killed by immersion in hot water at 55°C. for two minutes (Theron 1945). Where parasitized, paralyzed hosts, and conditioned cocoons were set up in the experiments, female *Mastrus* other than those in the experiment tubes were used to effect such results.

Series 1: Unparasitized hosts alternated with parasitized hosts bearing parasite eggs.

Series 2: Unparasitized hosts alternated with paralyzed hosts, no parasite eggs have been deposited on the latter.

Series 3: Unparasitized hosts alternated with paralyzed hosts in unconditioned cocoons.

Series 4: Paralyzed hosts in unconditioned cocoons alternated with paralyzed hosts in conditioned cocoons.

Series 5: Unparasitized hosts alternated with coddled hosts, both in unconditioned cocoons.

Series 6: Paralyzed hosts alternated with coddled hosts, both in unconditioned cocoons.

Figures for ten or more ovipositing females were obtained in each series and the results are given in Tables 1 to 6. In the first series the parasite eggs laid during the course of the experiment were separated from those present at the commencement by obvious differences in embryonic development. Statistical analysis by Snedecor's formula (1946) for group comparisons,

$$t = \bar{x} \sqrt{\frac{n(n-1)}{Sx^2}}$$

where $\bar{x}$ designates the difference between two group means, n the number of observations, and Sx^2 the pooled sum of squares, shows highly significant differences in behaviour in Experiments 1, 2, 3 and 5.

TABLE I

Oviposition of *M. carpocapsae* on unparasitized and parasitized hosts

	Experiment No.										Egg Totals
	1	2	3	4	5	6	7	8	9	10	
Eggs on unparasitized hosts	1	4	2	3	3	4	4	8	1	1	31
Eggs on parasitized hosts	0	2	0	0	0	1	2	1	3	0	9

$t = 2.90$; $P < .01$

TABLE II

Effect on oviposition of paralyzed hosts not bearing parasite eggs

	Experiment No.										Egg Totals
	1	2	3	4	5	6	7	8	9	10	
Eggs on unparasitized hosts	4	3	3	3	8	4	4	5	3	2	39
Eggs on paralyzed hosts	1	0	0	0	2	1	2	2	4	1	13

$t = 3.94$; $P < .01$

Experiment one establishes the fact that female *M. carpocapsae* possess the ability to avoid laying on parasitized hosts, even those bearing parasite eggs. Although no specific tests were made, it is reasonable to assume that this faculty would apply also where the parasite is in larval stages.

Experiment two establishes that whatever the deterrent factors limiting superparasitism, they do not appear to be associated with the presence, within the codling moth cocoon, of a parasite egg (or larva).

Experiment three shows that any conditioning of the cocoon by earlier ovipositing females is of no consequence in restraining oviposition, and the data, taken with those of the preceding experiment indicate that the really significant factors causing rejection of parasitized hosts are associated with the condition of the codling moth larva itself. This unimportance of any surface conditioning of the cocoon is confirmed by Experiment four where the female *Mastrus* treated alike paralyzed hosts in fresh and contaminated cocoons. There is a possibility that egg laying is accompanied by deposition of some characteristic secretion from one of the accessory glands, and that this chemical residuum is detected by subsequent females. This effect has not been entirely eliminated in the preceding experiments but the similar behaviour of the females in Experiments one and two give little or no support to the hypothesis.

The more obvious change in the parasitized host as compared with the unparasitized is in its paralyzed condition. Generally injection of the venom

TABLE III

Effect on oviposition of replacement of conditioned cocoon of paralyzed hosts by unconditioned* cocoon

	Experiment No.										Egg Totals
	1	2	3	4	5	6	7	8	9	10	
Eggs on unparasitized hosts	3	3	3	1	3	3	6	4	4	5	35
Eggs on paralyzed hosts in unconditioned cocoons	3	1	0	0	0	0	4	3	1	0	12

$t = 3.51$; $P < .01$

*See text for explanation.

TABLE IV

Oviposition on paralyzed hosts within conditioned and unconditioned cocoons

	Experiment No.										Egg Totals
	1	2	3	4	5	6	7	8	9	10	
Eggs on paralyzed hosts in unconditioned cocoons	1	2	3	5	2	1	0	2	3	0	19
Eggs on paralyzed hosts in conditioned cocoons	0	2	1	1	1	5	4	3	0	2	19

$t = 1.40$; $P > .23$

TABLE V

Oviposition on unparasitized and coddled hosts in unconditioned cocoons

	Experiment No.										Egg Totals
	1	2	3	4	5	6	7	8	9	10	
Eggs on unparasitized hosts	3	3	3	2	6	2	0	3	2	2	26
Eggs on coddled hosts	1	1	1	1	2	1	2	0	0	0	9

$t = 3.19$; $P < .01$

TABLE VI

Oviposition on paralyzed and coddled hosts in unconditioned cocoons

	Experiment No.																				Egg Totals
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Eggs on paralyzed hosts	0	1	1	1	2	2	1	2	1	1	2	0	1	2	0	1	1	3	2	4	28
Eggs on coddled hosts	1	1	3	3	0	0	4	8	1	2	1	1	0	0	2	1	1	3	2	1	35

$t = 0.73$; $P > .47$

by the female rapidly produces a cessation of locomotor activity but for a longer or shorter time there may be localized uncoordinated fibrillations in the abdomen etc. until these gradually diminish to give way to a flaccid paralysis. In typical cases the heart remains unaffected. At the same time it has been observed in the course of this work that the effectiveness of the stinging was rather variable, close confinement of the females with too many hosts perhaps causing depletion and weakening of the poison. Similar variation in venom effectiveness was reported by McClure (1933). Since lack of movement is a notable feature of the paralysis, some indication of the significance of the stimulating influence of movement of the normal host may be observed by supplying the females with coddled hosts as shown in Experiment five. The behaviour in rejecting such dead hosts, completely immobile to the observer, appears to be of the same order as that shown towards parasitized or paralyzed hosts. Confirmatory evidence of this appears in Experiment six where females oviposited as readily on paralyzed hosts as on those already dead. Host movements may thus be of exceptional importance in the exercise of the discriminatory faculty of *Mastrus carpocapsae*, although they are not necessarily the only stimuli eliciting this response.

It is already evident from Experiments one and two that the stimuli normally responsible for the rejection of parasitized hosts in this species are not directly associated with the act of egg laying (nor probably with the later presence of immature stages on the codling moth larvae) but rather are attributable to effects of the act of paralysis. The significance of Experiments five and six lies in the demonstration of an experimental simulation of these effects in hosts without

involving any sort of prior activity on them by female adults. These results reinforce the conclusion from Experiment three that chemical traces left by previous females are *not* the important causal factors of such reactions. Beard (1952) in his study of the toxicology of the venom of *Microbracon hebetor* Say made an interesting observation bearing on this behaviour. This worker was surprised to find that the usually acceptable *Galleria* larvae were avoided by *Microbracon* females when they had been D.D.T. poisoned. Since these latter hosts exhibited characteristic D.D.T. tremors Beard concluded that "abnormal movement of the host discourages them, rather than there being any perception on their part of a situation that would be deleterious to themselves or their offspring." However, it is known that this parasite in some degree does avoid oviposition on parasitized hosts so there is a slight possibility that the neuromuscular upset caused by injection of D.D.T. approximates conditions under which the discriminatory mechanism is brought into function. The question as to whether functionally similar behaviour patterns of the types shown above can always be referred to as the same causal mechanism is, of course, one which constantly puzzles students of animal behaviour.

Before passing to a discussion of these results, attention should be drawn to the ease with which superparasitism occurred in this species under the techniques employed. Advantage was taken of this by Simmonds (1944) to increase laboratory production of this ichneumonid on so-called unnatural hosts.

Discussion

The main objectives of the present work, the demonstration of a discriminatory faculty in the external parasite *Mastrus carpocapsae*, and the evaluation of the significance of chemical traces left by earlier ovipositing females on the host covering etc. as a deterrent to oviposition by subsequent females, have been attained by the above short series of experiments.

This parasite is able to distinguish between unparasitized and parasitized hosts, with the rejection of the latter related to conditions of the codling moth larvae rather than surface conditions on cocoons. Cocoons through which female parasites had oviposited two hours previous to the experimental periods had no apparent influence on the behaviour of subsequent ovipositing adults so that in this species the inhibiting effects, if any, of chemical traces left on the cocoons can only be of such brief duration as to be of little significance in regulating the incidence of superparasitism. From the standpoint of accessibility to female parasites it may reasonably be claimed that there is no essential difference between hosts cocooned as in the present example and hosts contained in various thicknesses of any type of plant tissue. The findings here reported therefore serve to confirm those of Narayanan and Chaudhuri (1954), who showed that adult parasite conditioning of sugar cane stalks used to enclose *Chilo zonellus* (Swinh.) larvae had no apparent effect on oviposition by *Stenobracon deesae* (Cam.). Salt's suggestion (1937) that certain types of behaviour observed as tending to reduce superparasitism by *T. evanescens* might also apply with parasites attacking hosts enclosed in plant tissues receives no support from the above data.

The method by which *Mastrus* females discriminate between unparasitized hosts is not demonstrated by the foregoing experiments. But there is a particularly interesting indication that the females, in rejecting parasitized hosts were responding to stimuli other than those consequent upon oviposition or the later presence of immature stages on the codling moth larvae. The similarity of the oviposition behaviour when females were confronted with coddled or parasitized

hosts in the presence of normal unparasitized ones, points to a common possession of the responsible stimuli by the two former types of host larvae. Or is it the simple absence of the appropriate stimuli to produce stinging and paralysis, which act in itself is an intrinsic component of the mechanism of discrimination? The latter hypothesis merits examination.

A noteworthy feature of the *Mastrus* behaviour shown by the data in the tables is that the ability to distinguish parasitized from unparasitized hosts was subject to such control or modification by operation of other factors as to result in abundant superparasitism. During the exposure periods selected for the experiments the amount of oviposition by groups of ten females in tubes containing all parasitized or paralyzed codling moth larvae did not differ significantly from that in tubes where 50% of the hosts were unparasitized (compare tables 1 and 4). What has been termed restraint in parasite oviposition behaviour was virtually absent even though the exposures were for the short duration of eight hours, a relatively brief interval in the average 30 day life of a *Mastrus* female. The behaviour in the complete series of experiments may be adequately interpreted by postulating that the threshold of stimulation for injection of venom was not reached where codling moth larvae were already paralyzed or otherwise rendered relatively immobile. Stimuli received from these latter hosts were only those releasing the oviposition mechanism—provided, of course, that the mature eggs ready for deposition were present in the oviduct. It was suggested above that host movements might be significant releasers in discrimination behaviour but other host characteristics could well be involved. The response is probably to multiple stimuli and the receptors chemotactile, olfactory and auditory, but there are obviously limits to their sensitivity. If we accept the definition of Pumphrey (1950) that "an animal hears when it behaves as if it has located a moving object (a sound source) not in contact with it", the theory that *Mastrus* females tend to avoid parasitized or paralyzed hosts on the basis of sound discrimination has a certain plausibility. The same author has aptly remarked that the deaf and dumb insect is exceptional, and although chordotonal organs are usually absent in Hymenoptera, the tarsal and tibial concentration of end organs is pronounced and their sensitivity to displacements of the substrate is probably much greater than to displacement of the air. No studies on this aspect of parasite behaviour are known to the writer. The assumption of Varley (loc. cit.) that recognition of parasitized hosts by a sense located in the ovipositor could not easily be used by ectoparasites may be correct, but avoidance of superparasitism by parasites laying outside hosts is not necessarily dependent on the receptors known to be used by endoparasites.

The act of host paralysis is clearly of considerable importance in some phases of host selection by this parasite. While it is probably safer to assume that all external parasites do not react in the manner of *M. carpocapsae*, behaviour recorded here can serve to clarify observations of earlier workers on the excessive superparasitism by externals under laboratory and field conditions, (Varley, loc. cit.; Theron, loc. cit.). External parasites almost invariably paralyze the hosts before egg laying, and quite possibly such paralyzed or parasitized hosts are only perceived by the females as media for egg deposition. Superparasitism in these types then becomes a function of complex temporal sequences of paralysis and oviposition, depending not only on the physiological rhythms of venom production and egg maturation, but also on the histories of individual females, host population densities, etc.

Ullyett (loc. cit.) recognized paralysis and oviposition as two distinct phases of parasite activity, and although he postulated periodic alternations of host

searching for paralysis with those of oviposition as an explanation of some of his experimental results with *Microbracon hebetor* Say and *Cryptus inornatus* Pratt, he at the same time thought that the phenomenon might be a laboratory artifact having no relation to field conditions. Nevertheless his descriptions of the actions of these two parasites appear to be typical examples of instinctive behaviour as interpreted by the Lorenz school (Tinbergen 1951). This school stresses as characteristic basic components of instinct, appetitive and consummatory actions, the former consisting of the variable striving or searching phase and the latter the rigid motor end response. Because Lorenz's ideas have gained wide acceptance and bear on problems of host parasite relations, investigations to establish the precise relationships between host paralysis, host finding, oviposition and discrimination deserve increased attention by biological control workers.

Summary

Details are given of the oviposition behaviour of *Mastrus carpocapsae* Cushman, a solitary external parasite of cocooned larvae of the codling moth, *Carpocapsa pomonella* L., in California and other parts of North America.

Tests to examine discrimination between unparasitized and parasitized hosts and assess the nature of such rejection, demonstrated that this parasite has such ability. In the presence of normal unparasitized hosts females usually avoided oviposition on hosts bearing parasite eggs, hosts simply paralyzed, and hosts coddled and killed by immersion in hot water for two minutes at 55°C.

Deterrent factors limiting superparasitism are shown to be related to conditions of the codling moth larvae rather than surface conditions on the cocoon. The rejection of parasitized hosts is apparently caused by stimuli other than those consequent upon oviposition or the later presence of immature parasite stages on the codling moth larvae. Similarity in oviposition behaviour towards paralyzed and coddled hosts suggests that discrimination may be on the basis of sound, with the act of host paralysis an intrinsic component of the discriminative mechanism. It is recognized that other host characteristics may be involved and the responses one to multiple stimuli.

The bearing of the results on previous demonstration of excessive superparasitism in external parasites is discussed.

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Observations on the North American Form of *Amphorophora rubi* Kalt. (Homoptera, Aphididae)

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In 1937 Schwarze and Huber (3) reported the variety of *Rubus idaeus* L named "Lloyd George" to be totally resistant to the aphid *Amphorophora rubi* Kalt. This fact was of some economic significance because the aphid in question had been shown to be an active vector of *Rubus* viruses in North America. It was suggested that the aphid-resistant qualities of Lloyd George should be incorporated in plant-breeding programmes with a view to producing hybrids, with desirable commercial qualities, which would escape infection by the viruses.

These findings did not agree with observations made in Great Britain. It has been known for many years that *A. rubi* is able to live and multiply in large numbers on Lloyd George. In recent experiments investigating the resistance of raspberry varieties to this aphid, the writer has shown that Lloyd George is, in fact, one of the most susceptible varieties to *A. rubi* in Britain. These conflicting results seemed to indicate that either the American variety Lloyd George differed from that grown in Britain—a point not corroborated by investigations into its history—or that the aphid in North America differed from its counterpart in Europe. The latter seemed the more likely explanation.

During a short visit to British Columbia in June 1955 the opportunity was taken to investigate this interesting problem. Through the kindness of Dr. R. Stace-Smith of the Canada Department of Agriculture, Plant Pathology Laboratory at Vancouver, raspberry plants of three European varieties were grown from root cuttings sent from the Scottish Horticultural Research Institute at Mylnefield, Invergowrie. The varieties were Lloyd George, Malling Promise, Malling Landmark.

On each of three plants of these varieties one late final instar nymph of *A. rubi* was placed and enclosed in a small bivalve cage, Hill (1). The aphids

were placed on young leaves of closely comparable age and therefore it is assumed of comparable physiological condition. After ten days the cages were opened and the progeny counted. A further count was made two days later. Unfortunately daily counts could not be made due to other activities in the field. These records are given in table 1.

Varieties	Totals of aphids on three plants of each variety	
	1st Count	2nd Count
Lloyd George	0	0
Malling Promise	3	3
Malling Landmark	43	46

The results clearly show that the North American form of *A. rubi* is unable to survive and breed on Lloyd George plants recently brought from Britain, thus confirming the earlier observations. It is interesting to note that although on Malling Promise a very slight degree of reproduction did take place, this variety is to all intents and purposes also resistant to the aphid. In Britain also the writer has never been able to demonstrate any statistically significant difference in the breeding behaviour of *A. rubi* on Lloyd George and Malling Promise. The totals of nymphs produced, rates of development of nymphs, daily reproduction rate and longevity of adults on both varieties has always been closely comparable (unpublished work). On the other hand the variety Malling Landmark which supported the North American form well, has proved to be almost completely resistant to the European form, Kronenberg, De Fluiter (2), Hill, (unpublished). Only in early Fall can the aphid breed on this variety and even then it does so with difficulty. It has in a few isolated cases bred earlier in the season on senescent leaves of Malling Landmark but, in the writer's experience, its fecundity, reproductive rate, adult longevity and nymphal survival rate were all of a very low order.

These results, while apparently confirming previous suspicions that *A. rubi* exists in more than one form, pose the interesting question of what is the nature of resistance in the raspberry plants to the aphids? Presumably it is of a physiological nature as evidenced by the seasonal changes in resistance of Malling Landmark to it in Europe. Hitherto it has been assumed that this variety either possesses some constituent which is inimical to the well-being of the aphid or else it lacks some essential factor required by the insect. However, the fact that the same variety in very comparable environmental conditions supports one form of the insect but not the other form, not only is puzzling but indicates clearly how little is known about the inter-relationship of aphids and their food plants.

Specimens of the North American race of *A. rubi* were collected in Canada during 1955 for the purpose of making a comparative study of them with the European form to see whether any morphological differences can be detected.

The writer wishes to express sincere thanks to Mr. W. A. Ross for making arrangements for him to work at Vancouver and to Dr. R. E. Fitzpatrick for placing at his disposal the facilities of the Plant Pathology Laboratory. Thanks are especially due to Dr. R. Stace-Smith for raising the plant material and for collaborating in the collecting of the insects in the field. To Dr. Conway A. Wood of the Scottish Horticultural Research Institute thanks are due for assembling and mailing the root cuttings. While visiting Canada the writer held a Travelling Scholarship from the Carnegie Trust for the Scottish Universities and a W. K. Kellogg Travelling Fellowship. To these organisations grateful acknowledgement is made.

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Note on *Sipha agropyrella* Hille Ris Lambers (Homoptera: Aphidae), an Aphid New to North America

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On June 20, 1950, aphids were collected from grass on the Tantramar marshes at Middle Sackville, N.B. The aphids were causing serious damage and turning the grass brown. The writer was unable to place the aphid in a genus according to Hottes and Frison (1931), Gillette and Palmer (1931), or Baker (1923). However, according to Baker (1920) and Theobold (1929) the aphid would fall in the genus *Atheroides* Haliday, on the basis of the shape of the cauda. It differed from the descriptions by Laing (1920) and Baker (1920) of the genus *Atheroides* in that the cornicles were prominent. In February, 1955, several specimens of the aphid were sent to Mr. J. P. Doncaster, British Museum of Natural History, who (in litt.) determined the specimens as of *Sipha agropyrella* (H.R.L.). Dr. Hille Ris Lambers, Bennekom, Holland agreed (in litt.) with this determination.

According to a publication by Hille Ris Lambers (1947), until recently unknown to the writer, the shape of the cauda cannot satisfactorily be used for the classification of the Chaitophorinae. He places the species living on Graminae and Cyperaceae in the subtribe Atheroidina, which includes the genus *Sipha;* those on Salicaceae and occasionally on *Betula* in the subtribe Chaitophorina; and those on Aceraceae and sometimes Hippocastanaceae, in the subtribe Periphyllina.

Borner (1952) places *S. agropyrella* H.R.L. in the genus *Rungsia* Mimeur. According to him the species of the genus *Rungsia* have a rounded cauda and those of the genus *Sipha* a knobbed cauda. He considers the species as a synonym of *Sipha kurdjumovi* Mordvilko.

Since 1950 this aphid has been collected in large numbers in New Brunswick from various host plants and from aerial traps. It has been collected from *Agropyron repens*, *Plantago major*, *Lycopersicum esculentum*, *Phaseolus vulgaris*, and *Nicotiana* sp. Winged and wingless forms were collected from June to October. In 1954 oviparous females and males were collected and eggs laid on *A. repens* in October and November at Fredericton. Collections were made at Middle Sackville, Cape Tormentine, Fredericton, Woodstock, Escuminac, Lincoln, and Maugerville, New Brunswick. It is easily recognized by its five-segmented antennae.

Hille Ris Lambers (1939) states that the species lives on *Triticum repens* and its allies and is common in the Netherlands, Italy, and Germany. Taylor

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and Gair (1954) record the species from *Arrhenatherum elatis* and *Agrostis stolonifera* in England.

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Book Review

THE BLOWFLIES OF CALIFORNIA (Diptera: Calliphoridae), by Maurice T. James. Bulletin of the California Insect Survey, Volume 4, No. 1. 34 pp. 1 fig., 2 pl. (offset printing) University of California Press, Berkeley 4, California. Published Oct. 28, 1955. Price 50 cents.

This paper records 16 genera and 37 species of Calliphoridae. It is the fourth on Diptera to appear in this Bulletin series and the method of presentation follows rather closely that of previous accounts, by other authors, dealing with Tabanidae, Culicidae and Itonididae. The introduction, which includes notes on biology, economic importance, family characters, terminology, and main literature sources, is followed by diagnostic keys to genera and species (adults only). Basically, the classification follows Hall (Hall D. G. The Blowflies of N. America. *Thos. Say Foundation.* 1948) but a revision of *Melanodexia* Will. is presented, with *Melanodexiopsis* Hall included as a synonym.

The construction and content of the work suggest to this reviewer that it is not intended to be a primer for non-specialists, but rather a presentation of the author's considered views on the value of the key diagnostic characters used by Hall and other students, with reference to the fauna of the western United States. The lack of even brief descriptions of species makes it an unsuitable work for beginners as does the evident non-emphasis on illustrations. The latter include, however, two excellent figures of the important structures at the base of the wing, reproduced from a previous work by the author. The body of the text consists mainly of California distribution records, and it is evident that an enormous quantity of material has been examined. It would have done no harm either to the author's intention or to the reader's feelings if this mass of data had, at least for several of the very common species, been presented in the form of maps.

G. E. Shewell.

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